# STUDIES IN MONOCARPIC SENESCENCE OF PLANTS

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Certified that the research work incorporated in the thesis entitled " STUDIES IN MONOCARPIC SENESCENCE OF PLANTS " which is being submitted by Mr Ruhul Islam Khan, M Sc for the degree of Ph D of this University, is an original piece of work done by him in this Department under my guidance and that the results of the present investigation or a part thereof have not been published or submitted for any degree elsewhere by any other person.

It is further certified that during the tenure of his research Mr Khan followed the rules and regulations as laid down by the University of Burdwan for the award of such degree.

( M A Choudhuri ) 31.1.91.

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# · Chapter−1 ·

# Review of literature on monocarpic senescence

## 1.1. <u>Introduction</u> :

Senescence may simply be defined as those deteriorative changes which lead, sooner or later, to the death of an organism or some part of it (377). Not only does senescence occur in almost all types of living organisms, it shows itself in different forms, even within the plant kingdom. In higher plants, single cell, group of cells or whole organs may be destined for senescence at what appears to be programmed times in relation to development of the plant as a whole. Unlike other developmental processes of the plant, senescence is the terminal phase of development.

There are two terms 'ageing' and 'senescence' which are widely used in reference to changes which impair the structural organization or functioning of living organisms. Whereas, senescence represents endogenously controlled active degenerative processes leading to death, ageing encompasses a wide array of passive or nonregulated degenerative processes influenced primarily by exogenous factors (207,287). This passive degeneration, termed ageing, is a consequence of lesions due to 'wear and tear' that accumulates over time and does not in itself necessarily cause death but may decrease resistance to stress or increase vulnerability to death (245, 287). Seeds in storage gradually lose their

viability and represent best examples of ageing (287). Thus, even if their developmental senescence programme is halted by preventing germination, seeds do not retain viability indefinitely. This degeneration may be due to gradual, time-dependent accumulation of lesions in DNA, the protein synthesising apparatus, membranes and probably other components of the cell (305, 426). There is reason to believe that these lesions are induced directly or indirectly by free radicals, reactive ions, and ionizing radiation, factors which occur naturally in our environment (330). However, our present knowledge is not good enough to define these processes more precisely or to draw a sharp distinction between them.

According to Osborne and Cheah (308), three important characteristics of senescence syndromes are : (1) progressive wear and tear with ageing and loss of ability to repair DNA breaks or lesions, (2) loss of membrane integrity and compartmentation, and (3) loss of homeostatic ability.

## 1.2. Types of senescence :

Cells are the basic unit of an organ or organism and it may be possible that all types of senescence are more or less alike (206) and basically similar at least at the cellular level (287), but the triggering actions may be different because death of a particular organ or a cell takes place at different stages of development. Leopold (206), on the basis

of morphological characters, has recognized four patterns
of senescence : overall senescence (e.g., monocarpic plants),
senescence of total aerial parts (e.g., perennial bulbous
plants), progressive senescence of leaves from base to apex
(e.g., bristle cone pine) and deciduous leaf senescence (e.g.,
winter shedding trees). Senescence occurs at different levels,
from individual cells to tissues to organs to whole plants
(206, 297). On the basis of this, Nooden (287) has recognized
four patterns of senescence : cellular, tissue, organ and
organism.

A somewhat different categorization of senescence beha-
viour pertains to flowering and fruition habit. Here we encoun-
ter monocarpic and polycarpic senescence. In the former,
senescence and death ensue after the plant has flowered and
borne fruits for a single time, this may not necessarily be
annuals. In the latter category, the polycarpic-type senescence
occurs only after many cycles of flowering and fruiting (451).
While senescence-related changes in different tissues or
organs of plants do show diversity, there are underlying
similarities, especially at the ultrastructural level, sugg-
esting that the processes of senescence are analogous (287).

Senescence of plant organs is a very common phenomenon
in nature and has a great positive value from the ecological
point of view. Organ senescence pertains to leaves (403),
roots (147), flowers (243), fruits (391) and seeds (305).

The pattern of leaf senescence is varying in nature and different parts of a single leaf senesce at different rates (382, 446). The leaves of graminaceous plants senesce progressively from apex to base. The tissue around the vascular bundle seems to senesce later (50, 323), also the sieve tube remains functional until very late (240), possibly for nutritional purpose. In rice cultivars, two types of leaf senescence behaviour are reported, namely, sequential and non-sequential (257, 258, 259).

Monocarpic plants are mostly herbaceous and undergo single cycle of reproduction, whereas, polycarpic plants are mostly perennial and undergo many reproductive cycles without intervention of death (153). According to Nooden and Leopold (291) monocarpic senescence is a carefully orchestrated retreat, rather than a plunge into chaos. Monocarpic senescence is the most remarkable post-reproductive development of the whole plant and exemplified by annual, biennial and even perennial plants. Some perennial plants, such as Agave americana (440), Corypha palm (169), bamboo (98) and some highly branched trees, e.g., Cerberiopsis candelabrum (425) and Tachigalia versicolor (108) exhibit monocarpic habit.

Short life span of most monocarpic plants has been harnessed by scientists for basic physiological research. It is for this reason that the mechanism of whole plant

senescence has been studied in short-lived monocarpic plants such as soybean (24,72,73,89,294,295,299), pea (122,135,210, 227,228), rice (30,31,32,257,259,339), wheat (35,39,151,237, 318,323) etc. Study of senescence in intact plant is particularly important since detachment not only removes the organ from the normal influence of correlative controls, but may prevent the normal exodus of nutrients that may be released during the senescence process, thereby causing their accumulation and modifying the pattern of changes taking place at the cellular level.

Most of the works on monocarpism were done on annuals or biennials owing to a number of advantages. It is easier to monitor changes associated with the development of senescence in monocarpic annuals and to tackle the whole plant for experimental purpose with greater ease, compared with polycarpic plants or long-lived monocarpic plants.

An overwhelming body of research reports on monocarpic senescence has accumulated over the last two decades and they have been comprehensively dealt with in a number of excellent books and reviews published in recent years (64, 97, 183, 208, 283, 286,290,291,297,307,351,377,491,452,453, 454). The earlier reviews on this aspect are those of Molisch (253), Leopold et al.(210), Janick & Leopold (168), and Nooden & Leopold (291). A number of physiological and

biochemical changes take place during ageing and senescence of a whole plant. A brief review of literature dealing with such changes will now follow.

## 1.3. Physiological and biochemical changes associated with leaf senescence :

### 1.3.1. Changes in photosynthesis and respiration :

During monocarpic senescence the leaves show a decrease in a wide range of physiological functions (281,291,410) and among them the decline in photosynthesis is the most important. The rate of photosynthesis gradually declines in attached and detached leaves during senescence of several species (117,220,221,271,397,452,456). It is well known that during senescence photosynthetic pigments are gradually degraded, but several workers have suggested that chlorophyll degradation is not directly correlated with the decline in photosynthesis during senescence (221,449). This is now strongly supported by the mutant of Festuca pratensis, where senescence occurs without chlorophyll degradation. Nooden (284) has concluded that photosynthetic capacity depends on the concerted actions of light and dark reactions. The degeneration of rubisco and other stromal enzymes during senescence is the important factor for declining photosynthesis (138,221,224,323,397,442). However, some reports indicate that rubisco activity may not be correlated with the decline

in photosynthesis (53,369,445). Along with the $CO_2$ fixing enzymes the rate of photosynthesis is greatly determined by ATP forming reaction or photophosphorylation, which declines during senescence (170,410). The rate of photosynthesis is modulated by supplying nutrients (310), water status (261) or by hormones (336,378) and removal of active sink organs, which greatly delays monocarpic senescence, but not in all species (8,65).

Senescence is an active, ATP requiring deteriorative process, and the respiratory activity is sustained till very late stage of senescence (291,345), increasing thereafter (364,401). Climacteric rise in respiration has been noticed during senescence of flowers and fruits (142), and in leaves (4). It may be assumed that the sustaining respiration during senescence serves to synthesizing catabolic enzymes (354) and also to export the resulting materials from the senescing tissue (297). During senescence of detached leaves, the respiratory quotient remains low, which indicates the combustion of amino acids produced from protein hydrolysis (351). ABA and BA promote and inhibit respiration and uptake of inorganic phosphorus, respectively, through uncoupling and coupling of oxidative phosphorylation (246,364,381).

## 1.3.2. Changes in nucleic acids and protein during senescence :

Nucleic acid and protein, two most important biomole-
cules, do regulate most of the physiological and biochemical
processes in plants. DNA content decreases during senescence
in both attached and detached leaves of several species (43,
55,94,145,420). However, opposite reports are also available
(16,225). It has been also reported that the number of copies
of DNA in plastome declines during senescence (199,367), which
may be the actual cause of decline in DNA in the leaf tissue
during senescence (197). Chang  et al.(55) have observed
that the repetitive sequence of DNA of cotyledonary nuclei
declines during senescence, while the other region remains
intact.

The total RNA content in the leaf tissue declines during
senescence of several plants (30,281,291,410). The different
types of RNA present in the cell are degraded in different
times and at different rates. Thus, m-RNA synthesis declines
during senescence of oat leaves,but some new m-RNA reappears
(226) and those are present in the senescent cells behave
quite differently from the early stages in the nature of
translation (437). The increase or decrease in the abundance
of t-RNA depends on the growth stage and physiological acti-
vity (326) and also in the nature of acetylation (327). The
chloroplast RNA is selectively degraded during senescence of
Perilla, cucumber and tobacco leaves (51,52,398). The loss

in RNA is due to increase in RNAse activity in detached
leaves (88,115), but such correlation between RNA level
and RNase activity was not observed in attached leaves
(194,291).

The breakdown of protein is the characteristic feature
and universal during senescence of cells, organs, or orga-
nisms (198,223,281,289,444). Such event, however, may be
delayed by supplying nutrients, hormones or by several
surgical treatments, having delaying effect on senescence
(99,223,443) in some but not in all species (65,137). Most
of the works have been done on leaf soluble protein, rubisco,
which greatly declines during senescence (112,222,443).
Also, the loss of membrane protein and cytochrome are
reported (50,347,408). Several reports suggest that the
loss in protein is due to concomitant increase in protease
activity (27,234,438), But Mae and Ohira (219) have observed
no such relationship in rice plant. Veierskov and Thimann
(424) have suggested that loss in protein is due to impair-
ment of vacuolar membrane which allows the protease to
attack in the cytosol and organelles.

It is now known that leaf senescence requires the
synthesis of specific senescence proteins in the cytoplasm
(410) and in the chloroplast (79,80,352,460). Chloroplasts
isolated from attached senescent leaves synthesize almost
exclusively several proteins that are different from those

synthesized in young leaves (114). Significantly, the inhibition of chloroplast protein synthesis retards the loss of chlorophyll and protein by senescent leaves (80, 236). However, just before leaf senescence there is an increase in the protein synthesis in chloroplasts (114,236). Martin and Sabater (235) have shown that kinetin controls chloroplast gene expression in senescent leaves at both the transcriptional and translational levels. Further studies indicate that early in senescence, the polypeptides of the envelope change, but that probably most of the new polypeptides are synthesized in the cytoplasm (136). The results of Guera et al.(136) further indicate association between the thylakoids and many of the proteins synthesized by senescent chloroplasts, which may be related to subsequent membrane lipid and pigment breakdown (454). According to Thimann (406) proteins that retard senescence are different from those which accelerate it.

Chromatin-associated histone and nonhistone proteins are also important in the regulation of gene action (191, 316,388). Petel and Berlyan (317) have observed a close relationship between DNA/histone ratio and RNA content. Decrease in HI histone has been correlated with transcriptionally poised chromatin structure (69). More subtle tissue-specific shifts in the ratio of histone variants have been demonstrated in numerous cases (186,279,388,433).

## 1.4. Ultrastructural changes in the leaf tissue during senescence :

The deterioration at the ultrastructural level of chloroplast, mitochondria and membrane has been observed during senescence. The degeneration of chloroplast has been reported in several species (28,117,454,455) and thought to be mediated by hydrolytic enzymes (83,238). Several reports suggest that the number of chloroplast decreases during senescence (199,443), whilst others indicate that it remains constant till very late stage of senescence as in wheat and barley (238,434). The stroma thylakoid is degenerated before grana thylakoid (133,280,409), which is evident from non-yellowing mutant of Festuca (408). The gradual increase in osmophilic granules in chloroplast is observed in several species (133,280,323,445) due to degeneration of thylakoid. Lastly, the envelope of the chloroplast is disrupted after complete deterioration of internal membrane system (144,455).

The mitochondria are more stable than the other cell organelles and their structural integrity is lost in the very late stage of senescence (214,345,348). The molecular events suggest that dismantling of mitochondrial membrane may be initiated by internal selective proteolytic enzymes, possibly triggered by conformational changes in the membrane protein. The protease attack on the membrane liberates amino acids which may possibly be the cause of sudden rise in respiration prior to senescence (348,455).

The most notable feature of senescence is the deterio-
ration of microsomal membrane resulting in loss of permea-
bility and selectivity (90,244,411,413), which permits the
release of substrates, cofactors, ions and hydrolytic enzymes
and disrupt the compartmentalization in the cell. Such events
enhance the dysfunction of cell or tissue. Three main causes
of membrane dysfunctions are : (1) change in phase properties
from liquid-crystalline to gel-crystalline phase, (ii) forma-
tion of bilayer lipid configuration and (iii) specifically
inverted micelles (244,411).

The coexistence of both phases alters the pattern of
protein organization, affecting enzymes (361) and renders
lipid bilayer highly permeable (15). Electron spin resonance
(ESR) and fluorescent depolarization studies of isolated
membranes from senescing tissue showed decrease in lipid
fluidity (244,412). The fat or fatty acids of membranes are
also lost during senescence (58) due to increase in phos-
pholipase activity. From such fatty acids, jasmonic acid,
a highly senescence promoting agent (362) and malondialdehyde,
a fatty acid degradation product (196,400), are produced
which are increased during senescence (177,319). Membrane
protein degradation is also an important feature of disman-
tling of membrane. The number of thiol groups per unit
membrane protein declines during senescence or there occurs
a selective loss in thiol-rich proteins (244).

## 1.5. Correlative control of whole plant senescence :

The different organs of plant form a complex system
which influences each other in a way that serves to achieve
a coordination of developmental processes (17,127,355). A
branch on a tree eventually dies along with the tree, but
if excised and rooted the branch becomes a full grown tree.
Also the longevity of leaves is greatly extended by excision
followed by rooting (59,253). In tissue culture, any cell
of a plant forms a new plant by nutrient and a balance of
hormone application. Thus, the genetic constitutents are
same in every cell, but selectively expressed by hormones
produced by different plant parts, which also regulate
mobilization of nutrients and physiological functions. Thus,
all the organs are interlinked and they regulate functions
of the whole plant in a correlative manner. Correlative
control also operates at the cellular level (17), the prime
case is the xylem differentiation (380).

Most successful approach to analyse correlative con-
trol has been the surgical methods. The excision of one
organ permits the analysis of its effects on the other.
It has been observed that pollination enhances senescence
of petals within a very short time (128,253), but inhibits
degeneration of ovary. In germinating seeds, cotyledons
deteriorate due to supplying of nutrients to the shoot
apex. Thus, removal of shoot apex delays cotyledon senes-
cence (26,270). The removal of roots promotes senescence

of leaves (284,432). Also, within a leaf the petiole may promote blade senescence and its removal extends the life- span of excised betel and Hibiscus leaves (248,251). In soybean, bean, rice and many other plants removal of repro- ductive structures retards senescence (257,289,291,421) but not in all species (8,65.137).

Shoot systems are more important in regulating whole plant senescence; the plant dies because the assimilatory organs senesce (282). This is strongly evident from the photoperiodic manipulation and root/shoot grafting experi- ments (282). Thus, it appears that supply of nutrients and hormones from leaves and roots is the prime factor in regu- lating whole plant senescence. The retardation of senescence by cytokinins, xylem differentiation by auxin, ABA dependent stomatal closure and regulation of root growth by auxin (288,452) suggest that hormones actually regulate all the physiological processes of whole plant as well as its sene- scence (32,127,209,339,435). Ambler et al.(10) have showed that nonsenescent Sorghum exhibits delayed leaf senescence due to correlative controls between root-produced hormones and shoot development. (And) nonsenescent Sorghum showed higher level of cytokinin (9).

From the available literature it becomes apparent that senescence of monocarpic plants is more amenable to analysis than senescence of polycarpic plants and therefore, we know

a great deal about monocarpic senescence. In most of the
cases but not always, the fruits, particularly the seeds,
have been shown to induce monocarpic senescence. A wide
range of degenerative changes occur during monocarpic
senescence, and, as already described, changes in one part
of the plant induce alterations of other parts of the plant.
In most monocarpic plants, the decline in leaf function and
shedding of the leaves seem to be particularly important.
The correlative effects, e.g., seed effects on the leaves,
may be mediated by hormones as well as other factors (97,
290). Many attempts have been made since the time of Molisch
(253) to explain the mechanism of monocarpic senescence,
But up to date no singular theory seems to be appropriate
and satisfactory enough to explain the general phenomenon
of this terminal developmental process, especially  the
triggering mechanism of the process.

Since the most remarkable phenomenon is the post-
reproductive senescence of the whole plant, i.e., monocarpic
senescence, we will discuss the present concept of the
mechanism of monocarpism.

## 1.6. Theories of monocarpic senescence :

Current reviews on plant senescence reveal that, although
a large number of studies on monocarpic senescence of plants
have been carried out, the actual mechanism of this process

is still far from clear and it appears that the process is
very much complex (64,97,183,208,209,210,281,283,289,290,
297,307,351,452,453). It also becomes fairly clear from the
perusal of these reviews that there exists considerable
discordance among scientists with regard to the mechanism
of senescence in monocarpic plants. Admittedly, one thing
appears certain that it is not merely a time dependent un-
controlled process, but a very much regulated self-destruction
process, where a dramatic degeneration occurs in an orderly
fashion following the reproductive development dictated by
the genetic programming of the species concerned.

Various proposals have since been put forward to explain
the mechanism of monocarpic senescence, which can be grouped
under the following four hypotheses : (i) the nutrient drain
hypothesis, (ii) the production of death signal by reproduc-
tive structures, (iii) the hormonal regulation of whole
plant senescence, and (iv) the nutrient stress-induced
hormonal disbalance leading to senescence. The available
experimental evidence in support of each hypothesis will be
cited and the relative merits and demerits of each hypothesis
will be discussed in the pages to follow. It may be mentioned
here that not a single hypothesis does provide sufficient
proofs for elucidating the actual mechanism and each has
got its own limitations.

## 1.6.1. (i) Nutrient drain hypothesis :

This hypothesis, put forward by Molisch (253), suggests that mobilization and drawing of nutrients and organic compounds from the vegetative parts (photosynthate from the leaves and hormones and nutrients from the roots) by the reproductive parts cause monocarpic senescence. According to this hypothesis a pull from the strong sink of young reproductive tissues monopolizes all nutrients, helped by a reduced sink strength of the vegetative parts of flowering plants. This hypothesis has recently been modified by Kelly and Davies (183) and has received renewed attention in recent years (139,182).

Working with G-2 line (photoperiod-sensitive) of Pisum sativum, Peter Davies and his coworkers (122,139,140,141,182) made significant contributions to our understanding of the influence of the reproductive structures on monocarpic senescence. In this genetic line, senescence does not occur in short-day (SD) despite fruit production and the accompanying nutrient drain to the fruits, which may be as great under nonsenescing as under senescing conditions. They have recently demonstrated that the rate of reproductive development as well as senescence are regulated by interaction of genes (Sn and Hr) and photoperiod (181). They have argued that delay of senescence in SD is due to reduced sink demand of the developing reproductive structures for

assimilates, resulting in more assimilates available for vegetative growth. The correlation of delayed apical sene- scence and greater assimilate supply to the vegetative structures has been demonstrated by Kelly and Davies (182). This observation supports some aspects of Molisch's proposal that fruits or seeds divert assimilates from the vegetative parts, triggering their senescence, when they received insufficient assimilates to survive.

Both the nutrient drain hypothesis and a hypothesis in which it is proposed that the reproductive structures produce and export a senescence signal (281), assign a central senescence-inducing role to fruits or seeds, no doubt, due to the observations that removal of reproductive structures delays or prevents senescence of many species (289). However, senescence of peas (343) and other species (289) has been reported in the absence of fruits, and argues against a central senescence inducing role for fruits and seeds. Moreover, in soybean, early senescence-like changes and loss of assimilatory capacity were independent of the pre- sence of fruits (47,74). These observations speculated that senescence was induced early in the reproductive phase, and was only enhanced by the fruits. The results provided by Kelly and Davies (182) also supported this conclusion. The effects of the senescence controlling genes were apparent
-in
on assimilate partitioning with/ the apical bud of G-2 peas,

long before fruits or seeds were present. It seems likely
that these genes mediate partitioning between primordia,
very early in reproductive development. Furthermore, root
growth (359) and assimilation by roots (202) have been found
to decline before the period of rapid pod growth in pea which
indicates decline in the sink strength of the vegetative
parts, which is associated with flowering, while the ability
of reproductive sinks to divert assimilates regulates
senescence. Kelly and Davies (182) further suggest that this
ability is conferred on reproductive sinks by, and regulated
by, the whole plant, starting early in the reproductive phase.
Providing different lines of evidence from experiments on
rice plant, Choudhuri and Mondal (64) have suggested that
senescence-inducing genes are expressed at the time when
floral differentiation takes place.

The current works of Hamilton and Davies (139) on the
quantitative export from fruits (140) and the identification
of the exported materials from the fruits as sucrose and
malic acid, have led them to abandon the concept of senescence
factor or signal. According to them the shift in nutrition
partitioning that is diverting more photosynthate and nutri-
ents to developing reproductive structures, causes less
nutrients available for continuing vegetative growth. As
seeds develop, the nutrient demand of the seeds leads to
the further reduction in nutrients available for continued
growth. Although this is not the cause of senescence, it

magnifies the already existing nutrient depletion of vegeta-
tive tissue, so that senescence takes place. It seems that
the mechanisms of monocarpic senescence are probably not
the same in various plants, with small differences between
the species and large differences between the plant families.

### 1.6.1.1. Sink strength, mobilization and senescence :

The conspicuous growth of the reproductive apices after
being transformed from vegetative apices, seemingly at the
expense of the vegetative structures, and the close correla-
tion between seed-filling and monocarpic senescence,  lend
credence to the concept that death is a consequence of exhaus-
tion and starvation due to a massive export of nutrients to
the developing fruits (32,35,39,253,259,339,383). It is
observed that senescence in mature plant parts is influenced
or enhanced by young growing organs (320,283,341). As the
individual leaf develops and ages, they switch over from net
importer of metabolites to net exporter (419). It is now well
recognised that source-sink interactions are complex, because
the plant may adjust itself as normal development progresses
or in response to experimental manipulations (75,116,161,290).
In particular, removal of reproductive structures not only
eliminates sinks and may delay senescence, but may also allow
alternative sinks to replace those removed (338,340,399).
Nevertheless, sink demand usually can influence the assimilatory

metabolism of supplier organs. Earlier recognition of the
differences among species and the variety of possible res-
ponses to source-sink alterations could have avoided much
unnecessary disagreement (290).

Adjustment of photosynthesis to sink demand has been
seen in many plants (290). This might be achieved through
changes in stomatal or mesophyll conductance, over the short
and long term, respectively, which may be mediated by ABA.
Normally ABA produced in the leaves flows to the fruits.
Hence, fruit removal causes ABA level to rise in leaves,
stomata to close (188, 189,373) and the photosynthetic machi-
nery to decrease in the leaf blades of many plants (337).
While a decrease in photosynthetic rate in a normal plant
is the senescence syndrome in monocarpic plants (287), it
may not accurately reflect senescence or it may be also
influenced by diminishing sink demand. The decline in photo-
synthesis, which results from the loss of photosynthetic
components (chlorophyll and RUBP case) rather than the
effects of sink loss, may better reflect monocarpic senescence
(289).

Although the redistribution of mineral nutrients from
leaves to developing fruits, particularly in monocarpic
plants, is the most striking example of redistribution,
exactly what regulates this is uncertain. Contrary to expec-
tations, redistribution, even for mobile nutrients such as

phosphorus and nitrogen, may be inhibited by a deficiency
in these elements or promoted by an abundant supply (281).
The experiments conducted by a large number of workers
suggest that interplay between the sinks (developing fruits)
and the sources (vegetative parts, especially leaves) is
more complex  than a simple withdrawal. However, the obser-
vations that fruits act as a powerful sink by virtue of their higher
hormonal level (48,76,84,85) than the leaves or other vegeta-
tive parts resulting in preference of movement of metabolites
to the reproductive structures, seems to strengthen the idea
of nutrient drain hypothesis. Although fruit development
influences the allocation of nutrients, the possibility that
root growth may be controlled by factor(s) other than metabo-
lite supply from the shoot cannot be ruled out either.

### 1.6.1.2. Stomatal conductance, reduced transpiration, mobilization and senescence :

Stomata regulate $CO_2$ exchange rates as well as trans-
piratory water loss. Stomatal conductance decreases with
ageing, which in turn, reduces photosynthesis and transpira-
tion (112,374,444). The xylem flux, in general, is controlled
by stomatal aperture which may, in turn, control transpiration
(289). However, in unstressed plant, stomatal resistance does
not increase markedly until quite late, that is, after redis-
tribution has progressed quite far and yellowing is about to

start (115,284) and, therefore, is unlikely to regulate
xylem flux as a prelude to monocarpic senescence. Several
studies have shown that the inhibition or acceleration of
leaf senescence is parallaled by changes in stomatal aperture
(315,403,404,407). Interestingly, cytokinin promotes stomatal
opening and retards senescence, whilst ABA produces opposite
effect (115,160,171,403). It is also in record that guard
cells remain viable and functional even when the mesophyll
cells are senesced (115,149,159,161). According to some authors,
the stomatal movement is controlled by factors external to
the guard cells (149,311). This speaks against stomatal regu-
lation of senescence. Another interesting observation is
that defruiting of wheat decreases stomatal conductance, but
inhibits leaf senescence (41), which may be an ABA effect
(215,373). Furthermore, Garrison et al.(115) have suggested
that rising stomatal resistance in maturing unstressed soy-
bean is rather a late event and may not be associated with
the initiation of senescence, since defruiting causes at
least a partial stomatal closure in soybeans yet inhibiting
monocarpic senescence (212,215). Hurng et al.(159) have
also demonstrated that stomatal closure is not directly
proportional to aging of rice leaf and that guard cells tend
to live longer than mesophyll cells. Since, stomatal closure
may actually accompany delayed senescence in intact plants,
other factors appear to be involved.

1.6.1.3. <u>Vascular architecture, mobilization and senescence</u> :

The vascular tissue (xylem and phloem) of monocarpic
plants plays a significant role in the mobilization of photo-
synthate from the leaves, and water, mineral nutrients and
hormones from  the roots. The work of Neumann and Nooden (275)
indicates that excision of seeds does not prevent transloca-
tion of $[^{32}P]$-phosphate out of the leaves, but transported
more in the stem and petiole instead of pods. Thus, the
vascular architecture seems to impose a preferential pattern
of translocation rather than an absolute restriction on move-
ment. The destruction by heat girdling of the phloem in the
petiole of the target leaf, a treatment which blocks with-
drawal of nutrients from the blades, does not prevent the
nearby pods from inducing senescence of that leaf (295). In
fact, the pod  causes senescence of the leaves; however,
supplying high level of mineral nutrients and cytokinin
through the xylem may override the action of the pods (115,
276,278,284). Thus, it appears that a decline in the flux  of
minerals and cytokinins from the roots via the xylem is
necessary for the pod to induce senescence (294).

Although depodding and phloem destruction in the petiole
prevent exodus of the foliar nutrients, there seems to be
some breakdown of foliar protein and resynthesis of other
proteins in cells along the veins (109). This further suggests
that hydraulic conductivity and the architecture of the xylem

are important factors, perhaps more important than stomatal
resistance, in determining partitioning via the xylem (269,
462). Martin (237) has observed that stem xylem is a possi-
ble pathway for mineral retranslocation from the senescing
leaves to the ear in wheat. He has suggested that a continuous
connection by sieve elements between leaves and grains in
wheat is not a prerequisite for mineral retranslocation.
Although, the arrangement of vascular tissue determines
redistribution of solutes, the structure of transport system
itself does not control, even though it may favour, the
movement from source to sink (247).

Orthostichous connections may restrict translocation of
photosynthate from leaves to fruits. Although very little
is known about orthostichous restriction of hormone movement,
the information on nutrient flux must also apply to other
regulatory factors which move in the vascular system (269).
Recognizing and analysing these connections seem essential
for understanding the mechanisms by which whole plants coor-
dinate the activities of their parts including monocarpic
senescence. Thus, it appears that although nutrient redis-
tribution may be a function of senescence, it may not
necessarily be the cause of monocarpic senescence.

1.6.1.4. <u>Control of senescence by nutrients</u> :

If mineral deficiency is one of the factors controlling
senescence, it is expected that applications by foliar spray-
ing of minerals could retard senescence. In fact, foliar
spraying of nitrogen (33,42), potassium (363), calcium (328),
boron (29) and manganese (33) have been found to retard leaf
senescence. Interestingly, some nonessential elements, such
as nickel (250) and cobalt (417) also retard leaf senescence.
In several cases these mineral elements have been found to
alter the endogenous hormonal levels (201,358,365). Some con-
tradictory effects have however been reported; neither appli-
cation of NPK to soybean leaf surfaces (372) nor force-feeding
via the xylem (242) prevented loss of these minerals from the
leaves. Similarly, foliar application of urea did not retard
chlorophyll loss in corn (23). All these observations point
out that inorganic nutrients may regulate senescence indirectly
possibly by modulating endogenous hormonal status, particu-
larly cytokinins, or changing enzyme activities, or both.

1.6.1.5. <u>Criticisms against nutrient drain hypothesis</u> :

The nutrient withdrawal theory of senescence has, however,
been questioned for some time (210,263,264,281,283,289,291,
297,299). Thus, in several dioecious plants such as hemp
(<u>Cannabis sativa</u>) and spinach (<u>Spinacea oleracea</u>), the male
plants senesce much like the female plants, even though they

do not form flowers and seeds and can, therefore, account
for only a limited nutrient drain to the reproductive
structures of the plant (210,264). It is also possible to
induce spinach plant to bolt by treating the plant with
gibberellic acid under short days forming a tall leafy
shoot (a massive sink) which does not form flowers. These
plants do not senesce if not allowed to form flowers and
seeds (168). In maize, the removal of reproductive parts
may accelerate senescence (8,65). Similar observations were
also made in oat (230) and <u>Capsicum</u> (137).

Fruit excision has been reported to increase endogenous
ABA level and stomatal resistance (215,374), which may be
one of the reasons for early senescence in these plants.
Krizek et al.(190) have shown that cocklebur senesces and
dies if the flower buds, formed under short days, are removed.
Thus, in this plant photoperiod-induced flowering rather
than seed development seems to control senescence.

Although removal of reproductive structures prevents
rapid death of many plants,such as soybean, pea, bean,
wheat, rice etc., many physiological and biochemical changes,
generally associated with senescence, are not prevented (289).
Decapitation of reproductive structures in male as well as
female hemp and spinach plants delay senescence (71,210).
Graftage experiments or photoperiod manipulation in soybean
and pea strongly suggest that the leaves and not the roots

or even the stem, appear to be the primary target of the
influence exerted by the reproductive structures in many
monocarpic plants (213,229).

Further evidence contradicting nutrient drain hypothesis
comes from the interbreeding experiments with pea cultivars.
Thus, it is possible to obtain recombinants which do not
undergo normal senescence and death following seed produc-
tion (239). The most significant contributions contradict-
ing nutrient drain hypothesis have come from the work of
Nooden and his coworkers at the University of Michigan.
They found that monocarpic senescence in soybean was in-
dependent of pod number (sink size) over a very wide range
(213,299). Subsequently, three lines of evidence based on
very different approaches have shown that the nutritional
requirements of the developing soybean seeds can be satis-
fied without sacrificing the plant if the assimilatory
capacities are maintained. The first line of evidence can
be provided from surgical experiments, that take advantage
of the limited mobility of the senescence signal, which
show that when the plants are modified so that the leaves
are not contiguous to the pods, the latter can develop
without killing the feeder leaves (213,282,299). Despite
the criticisms made by Woolhouse and his coworkers (377,431),
these experiments conducted by Nooden and his coworkers,
do separate seed development and leaf senescence. It was

also shown by Nooden et al.(299) that reduction of pod number also reduced seed dry weight and N accumulation roughly proportionately. Thus, the idea that dominant reproductive structures compete through a simple passive sink effects on nutritional flux, does not seem to hold good. The second line of evidence against this hypothesis is a nonsenescent mutant of soybean which seems to produce a normal load of pods without the usual breakdown of the plant's assimilatory apparatus (3). The third line of evidence provided by Nooden et al.(298) shows that foliar spray treatments with combination of auxin and cytokinin can override the senescence signal and prevent monocarpic senescence. Moreover, 'sink demand' does not correlate well with monocarpic senescence when different species are compared (383).

Taking advantage of the photoperiod control of monocarpic senescence in G-2 peas independent of pod development, Gianfagna and Davies (122) have shown that nutrient demand by the seeds does not in itself cause monocarpic senescence. Thus, from these results nutrient diversion does not seem to be a primary trigger of monocarpic senescence. Although the exact role of nutrient deficiency in senescence, whether by withdrawal or diversion, is not clear, it can be argued that nutrient deprivation plays a role as an important background factor (281,283,295).

## 1.6.2. (ii) Production of death signal by reproductive structures :

From the discussions made above one is tempted to think that there exists some mechanism by which reproductive structures act on the vegetative parts, particularly the leaves, and this influence has been termed as 'senescence signal' by Lindoo and Nooden (213) and 'death hormone' by Nooden and Leopold (291). This hypothesis proposes that a senescence factor, probably hormonal in nature, originates in the seeds and migrates to the leaves inducing their senescence. The postulation for a control mechanism of monocarpic senescence mediated by a 'death hormone' is strongly favoured by Nooden and his coworkers working with soybean (281,283,291,297). The first idea of signal hypothesis perhaps comes from the works of Leopold et al.(210) and Janick and Leopold (168) with spinach plant. The source of the signal according to these authors is the seed in most, but not all, of the monocarpic plants. However, little information is available on the behaviour of 'senescence signal' in species other than soybean.

The exertion of the influence of senescence signal seems to occur during very late pod fill in soybean; depodding even quite late in pod fill still prevented the rapid yellowing and quick death of the plant (213,299).

The movement of the senescence signal is restricted, though
clearly less constrained than the nutrients that support
pod development, for monocarpic senescence. Nooden et al.
(299) have also provided evidence that pod development can
be uncoupled from senescence.

It has also been shown that the senescence signal exer-
ted mainly on the leaves closest to an individual pod or
pod cluster (281). Beyond this, the senescence signal seems
to travel mainly downward, but stays within the same ortho-
strichy as the source pod (213,281). The main influence,
that on the nearest leaf, is not blocked by steam girdling
of the petiole thereby indicating that it is exerted via
the xylem (284,295). However, the fact that the signal mov-
ing downward is blocked by steam girdling of stem suggests
that it moves downward via the phloem.

Several criticisms of their findings have been offered
by Wang and Woolhouse (431) and Sexton and Woolhouse (377).
However, these have been recently refuted by Nooden (289).
It has been suggested (289) that the senescence signal
differs from florigen. Earlier works of Davies and his
coworkers on the apical senescence of pea (86,121-123) have
suggested the downward movement of senescence-inducing
substance from the fruit to the apex. As already stated
they are of different opinion now and conclusions derived
from their recent studies with pea support the nutrient

diversion theory. Kulkarni and Schawabe (193) have shown a
different transmissible senescence-inducing factor which
originates in the leaves of Kleinia articulata induced by
long-day photoperiod. This influence is less mobile than
the senescence signal of soybean. In an interesting study
with groundnut, Ghosh and Biswas (120) have provided evi-
dence in support of the senescence signal coming from the
aerial flowers which do not bear fruits. The removal of
aerial flowers caused lesser senescence in groundnut than
that of fruits developed from cleistogamous flowers, suggest-
ing that the aerial flowers exert more lethal effect on the
senescence than the fruits/seeds produced by the cleistoga-
mous flowers.

Assuming that neither ABA nor ethylene are death hormone
per se (292), little is known about the possible identity
of the putative death hormone. The case for a 'pea factor'
with a carboxyl group was weakened when the compound was
found to be sucrose and malic acid (139). Besides ethylene
and ABA, the other naturally occurring compounds, in at
least pea and soybean, with characteristics of death hormone,
are chloroindole auxin and jasmonic acid (97).

Thus, most of the available evidence support both
'death hormone' and 'nutrient drain' hypothesis, although
each cannot explain the mechanism of senescence in all
monocarpic plants. With the development of new and sophis-
ticated techniques, the riddle of death hormone may be
resolved in the years to come.

### 1.6.3. (iii) Hormonal regulation of whole plant senescence :

It is now becoming increasingly clear that senescence involves a shift in the balance of senescence promoting and senescence retarding hormones. Most of the plant hormones have been implicated in senescence and each one has been shown to have regulatory power over the development of this syndrome (289,351,403,453). Although a plethora of research reports is available to substantiate the view that hormones control the senescence process, the exact role played by the known hormones in triggering senescence is far from clear. Sabater (351) holds the view that plants have possibly evolved mechanisms for the control of senescence by hormones as they have evolved mechanisms for the hormonal control of their correlative development according to their genetic potentialities and to the changing necessities of the plant.

In order to assess the hormonal control of senescence one must know those hormones which affect senescence symptoms; changes in the endogenous concentration of the particular hormone during senescence and changes in tissue sensitivity of the particular hormone. The causative relationship between senescent organs induced by change in hormonal level and the observed symptoms of senescence must be established. Although a great deal of information on the hormone effects of senescence of detached leaves is

available, our knowledge on changes in hormonal level and correlative effects among organs of the whole plant is fragmentary.

There are a number of reports which indicate that endogenous level of auxin decreases with leaf age. Production of auxin by the leaf blade and a decline in the flux of auxin down the petiole have long been implicated in the control of leaf abscission (281). However, very little effort has been made to understand translocation or changes in endogenous level of this senescence regulator in soybean. The ability of the auxin transport inhibitor, triiodobenzoic acid, to increase the number of pods in soybean suggests that the auxin may be involved (113,152). It could be that auxin mediates the inhibitory effect of young pods on subsequent pod initiation (158). Treatment with auxin, especially the synthetic auxin, $\alpha$-naphthalene acetic acid (NAA), delays monocarpic senescence of soybean (167). Interestingly, a combination of auxin, such as NAA and cytokinin, such as benzyladenine, dramatically prevented monocarpic senescence in soybean (298). The fact that auxin retards foliar senescence in some, but not all species (291,309,403) and that auxin exerts the opposite effect, that is promotion of senescence during induction of xylem formation (380), have made it a dubious candidate as a regulator of monocarpic senescence.

The endogenous level of gibberellin has been found to
decrease with leaf age (60,107). Gibberellin may also be
synthesized in roots and decreased level of it may accele-
rate leaf senescence. The application of gibberellin can
also delay foliar senescence in many species, such as,
Tropaeolum sp. (60), Taraxacum officinale (107), Rumex sps.
(125,254) and Lemna trisulca (18). Apical senescence in
peas is delayed by gibberellins (329). However, foliar
application of gibberellic acid does not alter monocarpic
senescence in soybean (281). In most of the cases where
gibberellic acid retarding senescence, cytokinin is generally
less effective. It may be that gibberellic acid substitutes
for cytokinin in such species. Since the effect of gibbere-
llic acid is very much limited in the control of whole
plant senescence, its regulatory role on monocarpic senes-
cence seems doubtful.

Among the senescence retarding hormones, cytokinins
are the most clearly implicated hormone in senescence. Cyto-
kinins have their effects in attached as well as in detached
leaves (4 ,107,214,259,342,346). A variety of experimental
approaches has provided compelling evidence that cytokinins
can delay or even reverse senescence in excised organs,
particularly in leaves, and these observations have strongly
supported the contention that a reduction in endogenous
concentration of cytokinin in leaves is an important factor

in the initiation of senescence (297,351,403). Although the effectiveness of exogenous cytokinin treatment on attached leaves is less clear, cytokinin in combination with auxin can inhibit the seed-induced senescence of leaves in intact soybean plant (281,298). Purohit (332) could reverse ethylene-induced senescence in sunflower by kinetin treatment. There are, however, a few exceptions of senescence retarding effects of cytokinins (265,309). These results indicate that there is certain diversity of the hormonal mechanisms controlling senescence. According to Sabater et al.(353), cytokinins affect different senescence-related processes (chlorophyll and phosphate loss) independently, which suggests that cytokinin may prevent leaf senescence through multiple actions.

Many studies have provided evidence for the roots as a major and possibly the sole source of cytokinin production (211. 422). This root-produced cytokinin is a major factor in sustaining the leaf longevity (184,192,281). Long ago it was shown that longevity of excised leaf is extended by the formation of roots on these leaves (59,253). Stressed roots or root removal caused a foliar yellowing which could be relieved by cytokinins (278,281). To implicate the hormones further in whole plant senescence, it has been demonstrated that the flux of cytokinins from the roots is relatively high during vegetative growth and relatively low

during reproductive phase (281,422). Sabater (351) has
suggested that decreases in the level of cytokinin during
leaf senescence might be due to:(i) an accelerated cytokinin
metabolism in the leaves before senescence, (ii) an accele-
rated transport from leaves to the other structures, and
(iii) a decrease in the supply of cytokinin from the roots.
It has been rightly pointed out (451) that sufficient emphasis
has not been given on the interplay of different parts of
the whole plant and in particular, the profound changes in
the growth and metabolic activities in the roots as the
fruits develop.

Kao (175) has concluded that in soybean seedlings, the
leaf senescence is caused by a competition among leaves for
root cytokinins. In other species, however, removal of the
terminal and axillary buds or of the flowers increased flux
of cytokinins from the roots (21,68) suggesting that fruit
removal does not simply cause the elimination of source of
competition for cytokinins. Although changes in cytokinin
level generally correspond the leaf senescence, no correla-
tion has been found between  decrease in the fruit cytokinin
and leaf senescence in soybean (214). Conceivably, seeds do
not compete with the leaves for the supply of cytokinin (293).
This implies that root cytokinins are not possibly the pri-
mary causal factor in monocarpic senescence at least in
soybean. This is further substantiated by the observation

that the leaves of depodded explant of soybean do not
yellow even if cytokinin is not supplied (278); therefore,
cytokinin deficiency per se does not trigger foliar yellow-
ing in soybean.

Abscisic acid (ABA), the most studied hormone, plays a
great role in promoting senescence of leaves. ABA treat-
ment promotes senescence in detached leaves of many species
(22,291,389,403), whilst it does not accelerate senescence
in attached leaves of others (95,281). Lindoo and Nooden
(214) have shown that ABA accelerates senescence of podded
plant but surprisingly, not in depodded soybean. That the
age of leaf is an important determinant of ABA action is
evident from the works of Smith et al (386), who have demon-
strated that ABA has no effect on young attached leaf, while
accelerating senescence of mature attached leaf of cotton.
Several groups of workers have observed that ABA-like acti-
vities in leaves increase during the period preceding visi-
ble yellowing (32,60,214,259,339,360). However, no consistent
change in the ABA level has been found during the senescence
of primary leaves of Phaseolus vulgaris and field-grown
soybean (64,70). Other inconsistencies with ABA are: young
leaf containing more ABA than mature green leaves (281),
complete depodding (which prevents foliar senescence in
soybean) increasing foliar ABA level (373), and failure of
foliar ABA application to induce senescence of depodded
soybean (214). According to Nooden (289), high levels of

senescence retarding hormones such as cytokinins, which counteract the ABA in the leaves of younger or depodded plants, could be a cause of these discripancies.

Generally the leaves and not the roots are the primary source of ABA (429). However, ABA is likely to be produced in root cap which, in conjunction with IAA, perhaps modulates the root growth (451). According to Hartung (146) this ABA of root origin probably is not translocated to leaves. Reproductive structures generally show high level of ABA content (281). Interestingly, labelled ABA injected into the pods does not travel to the leaves in significant quantities at the time of senescence (296).

It is well known that stomatal closure and ABA level are closely associated in senescence. Depodding has been found to cause at least partial stomatal closure and accumulation of ABA in leaves (205,373,375), yet depodding can delay monocarpic senescence (299). Furthermore, Samet and Sinclair (360) have reported that ABA level increases in senescent leaves of soybean, after other processes have been initiated. Admittedly, ABA may not be the signal for monocarpic senescence at least in soybean. Still, ABA may play an important role in the senescence process of many other plants, may be in conjunction with other factors.

The role of ethylene as a regulator of abscission
(291), flower senescence (243) and fruit ripening (344,379)
is well established. With a few exceptions, the involve-
ment of ethylene in leaf senescence is still not clear.
The endogenous ethylene can hardly be a specific signal
for senescence induction since ethylene is produced in
every cell and may move from cell to cell by diffusion.
It is also well known that external application of ethylene
promotes leaf senescence. Although some reports are availa-
ble which have related changes in ethylene in leaves with
senescence (5-7,176,331,332), no consistent relationship
has, however, been established between ethylene production
and whole plant senescence. Furthermore, inhibitors of
of ethylene synthesis or action do not always prevent this
event. A number of reports suggests that there is a great
deal of interactions between ethylene and other phytohormo-
nes. Kao and Yang (176) have showed that ABA promotes sene-
scence, but significantly decreases ethylene production,
whereas, BA retards senescence but promotes ethylene pro-
duction in detached leaves. Both IAA and kinetin synergis-
tically stimulate ethylene production in the leaf discs of
tobacco (6). Sabater (351) has rightly pointed out that
little attention has been paid to the possible effect in
senescence of the well known high synthesis of ethylene
after cutting (2). Thus, it appears that endogenous ethylene

may play a role in senescence, presumably by interacting
with other hormones participating in leaf senescence.

Summarising the hormonal effects on senescence, it
seems plausible that the endogenous levels of various
phytohormones differ in different species and even in cul-
tivars (156), in different seasons, and also in leaves of
different   ages (64). Trewavas (418) has pointed out that
altering the concentration of a growth substance is not
the only potential regulatory mechanism in the control of
plant development,but it is the actual sensitivity of tissues
to growth substances which is an important determinant.This
would explain why different groups of growth substances
or metabolites elicit different responses in the same
tissue or organ at any time. But there is no definite
proof that any of the known plant growth regulators acts
as translocating signal in senescence. Thus, it is suggested
by Sabater (351) that it is more than one hormone, or the
hormonal balance, which controls whole plant senescence.

Woolhouse (451) has suggested how interaction between
organs may come to play in whole plant senescence. The
vegetative plant produces growth substances, such as IAA
and cytokinins, from the actively growing shoot and root
apiecs. The action of these substances perpetuates the
vegetative condition, But as the apex switches to differ-
entiating flowers, this 'feedback loop', is broken.

Again, as the leaves mature, the supply of IAA from the
apex is substantially reduced. This, in turn, diminishes
the supply of cytokinins from the roots as their growth
becomes less active. The general decline in regulators
that promotes the vegetative condition is accompanied
by an increase in regulators from the developing fruits.
This will include factors, such as that associated with
the expanding pods (senescence factor) and ethylene, which
promote senescence. They will also further modulate the
supply of regulators that promote the vegetative state,
thus,bringing about rapid senescence. Osborne (307) has
suggested that an array of growth promoting hormones,
nutrients and growth suppressing hormones appear to act in
concert to control the sequence of events in organ senes-
cence and to signal the onset of total organism senescence
leading to inevitable cell death. It seems, therefore,
more likely that a balance of growth promoters and growth
inhibitors rather than an individual hormone determines
the signal to overall senescence. If, however, the senescence-
inducing hormone is actually involved, it may not be one
of the known hormones.

### 1.6.4. (iv) Nutrient stress-induced hormonal disbalance :

Monocarpic plants are characterized by either having
all the vegetative apices transformed into determinate
reproductive structures (e.g., cereals) or having

indeterminate reproductive structures (e.g., pea, soybean etc.). Senescence processes in the monocarpic plants may take place in different organs at different times. Depending upon the presence or absence of reproductive structures, leaves of monocarpic plants followed two types of senescence. Thus, in absence of reproductive structures, the individual rice leaf senesces basipetally, i.e., the apical segment senesces first and then the basal part (172), because the growth of rice leaf is controlled by a basal meristem where the apical cells are older than basal cells. Again, senescence of intact leaf gradually starts from the bottom leaf and then proceeds in an acropetal order along the stem axis (257,339). Similar patterns are also shown by other cereals, such as maize (102). Further, the older the leaf, the lower is the level of photosynthetic efficiency and overall protein and nucleic acid synthesis. The dominance of the young over the old is thereby established so that the older leaves inevitably senesce and die first.

Neumann and Stein (277) have suggested that internally programmed changes in the hydraulic architecture of the plant progressively diverts xylem-transported root supplies of nutrients and cytokinins from basal to more apical leaves and thus possibly regulates the progressive senescence of leaves from the base upwards. Fraser and Bidwell (110) have suggested that successive leaves of a plant complete their

growth at different times and thus, begin their gradual decline independently. Murayama (267) has demonstrated that the death of lower leaves in rice is caused by the migration of nutrients from lower to upper leaves. A similar situation is also observed in maize (45).

Working with rice, Ray and Choudhuri (341) have suggested that the young growing vegetative parts can act as strong mobilizing centres for withdrawal of metabolites from the older senescing organs. Conceivably, the withdrawal of metabolites and mineral nutrients from the older leaves by the younger growing parts may cause a nutrient deprivational stress resulting in a hormonal disbalance (particularly in cytokinin and ABA) in them which seems responsible for the development of leaf senescence. The works of Choudhuri and his coworkers from this laboratory have provided strong evidence in favour of this hypothesis (32,257,258,259,339,340). Later studies by Biswas and his coworkers have corroborated this from their works with various types of plants (35-39).

From the studies of sequential and nonsequential mode of leaf senescence behaviour (257-259), it may be argued that the earlier senescence of the flag leaf in Jaya and Ratna cultivars of rice might be due to its close proximity to the reproductive structures. Had the reproductive structures communicated a senescence signal to the vegetative parts,

then the non-sequential mode of senescence would have been
a universal occurrence in rice and other cereals. But the
existence of the sequential mode of senescence in Masuri
and Kalojira cultivars of rice where the flag leaf senesces
later than the older second leaf, notCwithstanding the close
proximity with the panicle, strongly speaks against the
movement of senescence signal from the reproductive structures
to the vegetative parts leading to their senescence. Further
studies of Choudhuri and his coworkers suggest that the
withdrawal of metabolites may not be directly responsible
for the onset of senescence, rather it possibly creates a
situation (nutrient exhaustion) that would make the leaf
suffer a deprivational stress leading to a hormonal dis-
balance and eventually brings about senescence of the whole
plant (64).

Combining all the facts together, Choudhuri and Mondal
(64) have postulated a scheme of events to explain the
possible mechanism of monocarpic senescence in rice. The
scheme envisages that depletion of metabolites in leaves
due to export to grains imposes a nutrient-deprivation stress
in leaves leading to accumulation of ABA. This accumulation
ensures stomatal closure resulting in decreased transpiration.
This, in turn, reduces efflux of root cytokinin (162,163),
which is further compounded by the reduced synthesis of
cytokinin in roots during reproductive development of the

plants (21,384). Such a condition leads to an imbalance of
hormones in favour of possible ABA to cytokinin ratio (along
with senescence factor) that increases with the reproductive
development of the plant. All these conditions favour the
development of senescence syndrome and the plant eventually
succumbs to death. The change in balance from synthesis to
degradation can be viewed in cells of mature tissues as a
progressive decline in maintenance turnover of the process
of repair (307), But the most intriguing question remains
as to what triggers this process ?

## 1.7. Possible triggering mechanism of monocarpic senescence :

It is clearly evident that the reproductive structures
exert marked influence on the monocarpic senescence, but the
actual triggering mechanism of the process still eludes us.
According to Nooden (289) monocarpic senescence may be viewed
in terms of a preparatory and a final phase. The former in-
volves a decline or even cessation of vegetative growth
that renews the assimilatory organs and other tissues. Decrea-
sed mineral uptake and cytokinin production by the roots
may also be important components of the preparatory phase.
The massive decrease in the assimilatory activities and the
major redistribution of minerals invested in this metabolic
machinery seems to be part of the final phase (289). Most
of the available evidence fits both a death hormone hypo-
thesis and a nutrient drain hypothesis (97). According to

Choudhuri and Mondal (64), although mobilization of nutrients from the leaves to the fruits appears to hasten senescence, the actual trigger for the same at the genetic level perhaps comes at the time of floral differentiation. This can be corroborated from the observations that the duration of reproductive phase of different rice cultivars is fairly constant and the longevity of the cultivars varies due to variation in duration of the vegetative phase. Furthermore, the delaying of senescence of the whole rice plant either by removal of panicle or by application of hormones or nutrients could never be extended beyond a week or a couple and the senescence of rice plant could be deferred for about six months by preventing flowering by subjecting the photoperiod-bound rice cultivar to an unfavourable photoperiod in the field. Wangermann (432) observed that <u>Viola tricolor</u> dies following flowering or fruiting, but could over-winter in the vegetative  state if they did not flower. Osborne (307) reported that she could prevent senescence of <u>Xanthium</u> plant for as long as eight years by keeping it under unfavourable photoperiod. Likewise, prevention of flowering may allow monocarpic plants to reach a much greater size and age than normal. For example, avoiding the chilling required by cabbage and sugar beet prevents flowering, thereby allowing these plants to live more than two years and also to become very large (81,82). Under noninductive photoperiod,

soybean plants can be induced to last more than fifteen months (281). Thus, the flowering signal and not some influence from the fruits induce senescence. It may be mentioned here that apex senescence in pea may occur in the absence of flowering (343) but it has been argued by Nooden (289) that apex senescence and monocarpic senescence are different phenomena in the pea.

A number of dioecious plants show that the male plants senesce much like the female plants. The former dies after flowering even though they do not set fruits or seeds. All these observations strongly suggest that the induction of flowering actually triggers monocarpic senescence and that the formation of flowers and fruits is perhaps of secondary importance (321). As flowering is a prerequisite for all monocarpic senescence, it seems probable that the genes responsible for triggering monocarpic senescence being simultaneously expressed at the time of floral differentiation, and the senescence-inducing genes and flower-initiating genes are possibly linked together (64). However, the ultimate manifestation of the senescence syndrome may differ somewhat in different species. Sabater (351) has suggested that the transition from a hormonal equilibrium retarding senescence to another equilibrium stimulating senescence may be triggered by genes, including a marked change in the supply or in the synthesis of an individual hormone. However, the exact mechanism

of gene expression and the involvement of senescence
signal remains to be explored and there is a very good
reason to continue the research for death signal, although
their existence is certainly not yet proven beyond rea-
sonable doubt. Development of adequate techniques and
refinements of the methods can hopefully solve  the
problems relating to the programmed self destruction
process of the monocarpic plants in near future.

# · Chapter – II ·

# Studies in monocarpic
# senescence of plants

# INTRODUCTION

Monocarpy is very common in cultivated plants, especially in crop plants, such as cereals, which display the most dramatic form of overall senescence. The spectacular. event, which never escapes one's attention, is the sudden and synchronized death of plants in a cereal crop-field just before harvest time. In rice and wheat and other cereals, all the vegetative apices are transformed into reproductive structures at the time of switching over from one developmental phase to the other (64). These plants seem to serve as good experimental materials for studying the mechanism of monocarpic senescence, because here the source and sink are distinctly delimited and amenable to surgical manipulations and their life-span is also reasonably short for studying various changes generally associated with monocarpic senescence. The most characteristic feature of rice and wheat, which were used in the present investigation as experimental materials, is a special leaf, called the 'flag leaf', which emerges as the last leaf during the reproductive development. But the senescence behaviour of this youngest leaf is variable in different rice cultivars (257). Another characteristic feature of rice cultivars is that when the panicle is removed from the plant, a side branch

develops at the axil of the second leaf which alters the source—sink relationship, as also the senescence behaviour of the plant (257,339). Interestingly, such development of side branch could not be observed in depanicled wheat plant and hence there is no alteration in source—sink relationship in wheat as observed in rice.

As already emphasized in the review of literature (Chapter-I), that although a great deal of research has been carried out to elucidate the mechanism of monocarpic senescence in different plants, the nature of the actual trigger of the process is still not very clear and the process appears to be very much complex. However, if one goes through the current literature on this subject one will come to the inevitable conclusion that at present there are two hypotheses which are competing with each other to offer tangible explanations for the cause and effect of monocarpic senescence (97). Although the 'senescence signal' or 'death hormone' hypothesis has been well established in soybean (289) and is suggestive in some other plants (34,123,193), its isolation, characterization and mode of action are still eluding us. The other proposal, i.e., nutrient drain hypothesis, did not receive much attention since its postulation by Molisch (253), until recently. The publications from this laboratory on the mechanism of monocarpic senescence in rice (32,257,339) provided ample evidence in favour of the latter hypothesis, but

surprisingly that did not attract attention of the scien-
tists working in this area. With the recent publication by
Peter Davies and his coworkers (139-141,182) refuting their
earlier contention of the involvement of senescence factor
(signal) in the regulation of monocarpic senescence of pea,
the pendulum now seems to have started swinging back to the
nutrient drain hypothesis. In a recent review, Choudhuri and
Mondal (64) have postulated from a number of experimental
evidence that the genes responsible for inducing monocarpic
senescence are probably expressed at the time of floral
differentiation. It is interesting to record that the flower-
ing process is the common prerequisite for inducing overall
senescence in all types of monocarpic plants. The development
of fruits rather increases the sink demand, thereby deplet-
ing leaves of their nutrients and accentuating the death of
the whole plant.

In the present investigation attempts were made to
study various physiological, biochemical, hormonal and ana-
tomical parameters in a few rice and wheat cultivars showing
variations in their patterns of senescence during reproduc-
tive development, which may offer explanations to the diver-
gent patterns of senescence, particularly in some rice cul-
tivars. Furthermore, the correlative control of the process,
and the relative role played by the reproductive structures
were also analysed by altering the reproductive development

by various physical and chemical manipulative treatments
of the reproductive structures, particularly in rice culti-
vars. All these data embodied in the present thesis and
those published in the literature in respect of the whole
plant senescence taken together may lead to a proposition
which will hopefully throw light on when   and how the
induction of senescence in monocarpic plants is triggered
and the role played by reproductive structures in such an
event.

# MATERIALS AND METHODS

## 2.2.1. Plant materials :

   Several cultivars of rice (Oryza sativa L.) and wheat
(Triticum aestivum L.), which are widely used as staple food
throughout the world, were selected as experimental materials
for the present investigation. The rice plant is semiaquatic
in nature, whereas the wheat plant is totally terrestrial.
Both the plants are monocarpic, belonging to the family
Poaceae under the order Glumiflorae. In India, rice is culti-
vated from $8^{\circ}$-$30^{\circ}$ N latitude and under widely varying condi-
tion of rainfall, altitude and climatic conditions. The rice
plants are divided into two groups based on the response of
photoperiod to flowering; photoperiod-sensitive (season-bound)
and photoperiod-insensitive, the latter is grown regardless
of seasons. Wheat plants are mainly grown in the tropical and
temperate  regions between $30^{\circ}$-$60^{\circ}$ N and $25^{\circ}$-$40^{\circ}$ S. The
optimum temperature is about $25^{\circ}C$ and annual precipitation
ranges from 63-88 cm. In India wheat plant is mainly culti-
vated in Panjub, Haryana, Uttar Pradesh, Madhya Pradesh and
Bihar.

   For analysing the pattern and mechanism of monocarpic
senescence, six commonly grown rice cultivars namely, Rasi

(IET 1444), Sashyasri, Kalojira, Badsabhog, Patnai and Kalma
and two wheat cultivars, Sonalika and Kalyansona were taken
as experimental materials. Of these six rice cultivars, Rasi
and Sashyasri are short-statured and photoperiod-insensitive
(grown in the dry season), Kalojira and Badsabhog are medium-
statured and photoperiod-sensitive and Patnai and Kalma are
tall-statured and photoperiod-sensitive (grown in the wet
season).

### 2.2.1.1. Developmental stages of rice and wheat cultivars :

Rasi and Sashyasri rice cultivars have a good tillering
habit, attaining an average height of 79-82 cm. Anthesis of
these two cultivars takes place at the plant age of 94 and
82 days, respectively and crops are harvested after 133 and
122 days. Kalojira and Badsabhog have tillering habit lower
than the short cultivars and their average height is 101-105 cm.
Anthesis takes place at the plant age of 112 and 115 days,
respectively and crops are harvested after 152 and 156 days.
The tall cultivars Patnai and Kalma have good tillering habit,
their average height is 118-121 cm and anthesis takes place
at the plant age of 120 and 118 days, respectively. Crops are
generally harvested after 163 days. Of the two wheat cultivars
studied, Kalyansona has greater tillering habit ' than Sonalika;
anthesis takes place at the plant age of 56 and 64 days, res-
pectively and crops are harvested after 98 and 105 days, res-
pectively. The important phases of development period during

entire life cycle of all rice and wheat cultivars have
been given in Fig. A 1 & 2. The reproductive stage of all
the cultivars was divided into five stages, such as anthesis
(O day after anthesis or O DAA), grain-filling (O-7 days
after anthesis ˙ or 7 DAA), grain development (7-14 days
after anthesis or 14 DAA), grain maturation (14-21 days
after anthesis or 21 DAA) and senescent stages (21-28 days
after anthesis or 28 DAA).


## 2.2.2. Cultivation of plants :

Certified and healthy seeds of above mentioned rice cultivars
were collected from the Crop Research Farm of Burdwan University
and Rice Research Institute, Chinsurah, West Bengal, and wheat
cultivars were procured from Agricultural University, Pantnagar,
U.P., India. Seeds were surface sterilized in 0.1% (w/v)
mercuric chloride ($HgCl_2$) for one minute and washed throughly
several times in sterile distilled water. Seeds were then
germinated in plastic trays containing moistened blotting
paper at $37^oC$ in a germinator. The germinated seeds of rice
were sown in the seed-bed and 30-day-old seedlings were then
transplanted in the field in 5 $m^2$ plots, with one seedling
per hill at the spacing of 25 x 25 cm distance between plants.
On the other hand, germinated seeds of wheat were directly
sown in the field in 5 $m^2$ plots, in different rows at a dis-
tance of 45 cm between the rows and 15 cm between plants.
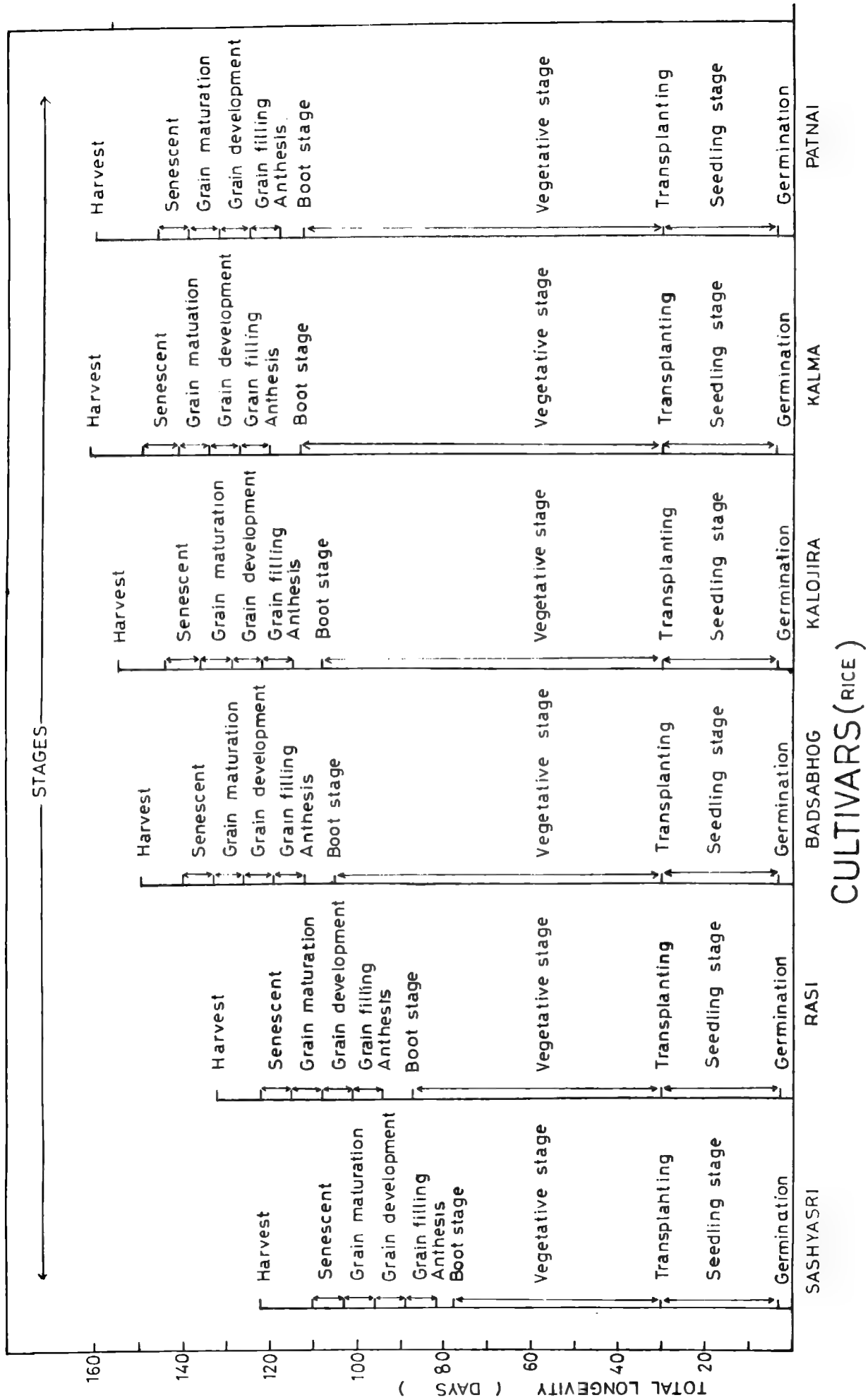
Fig. AI — Developmental stages of six rice cultivars.
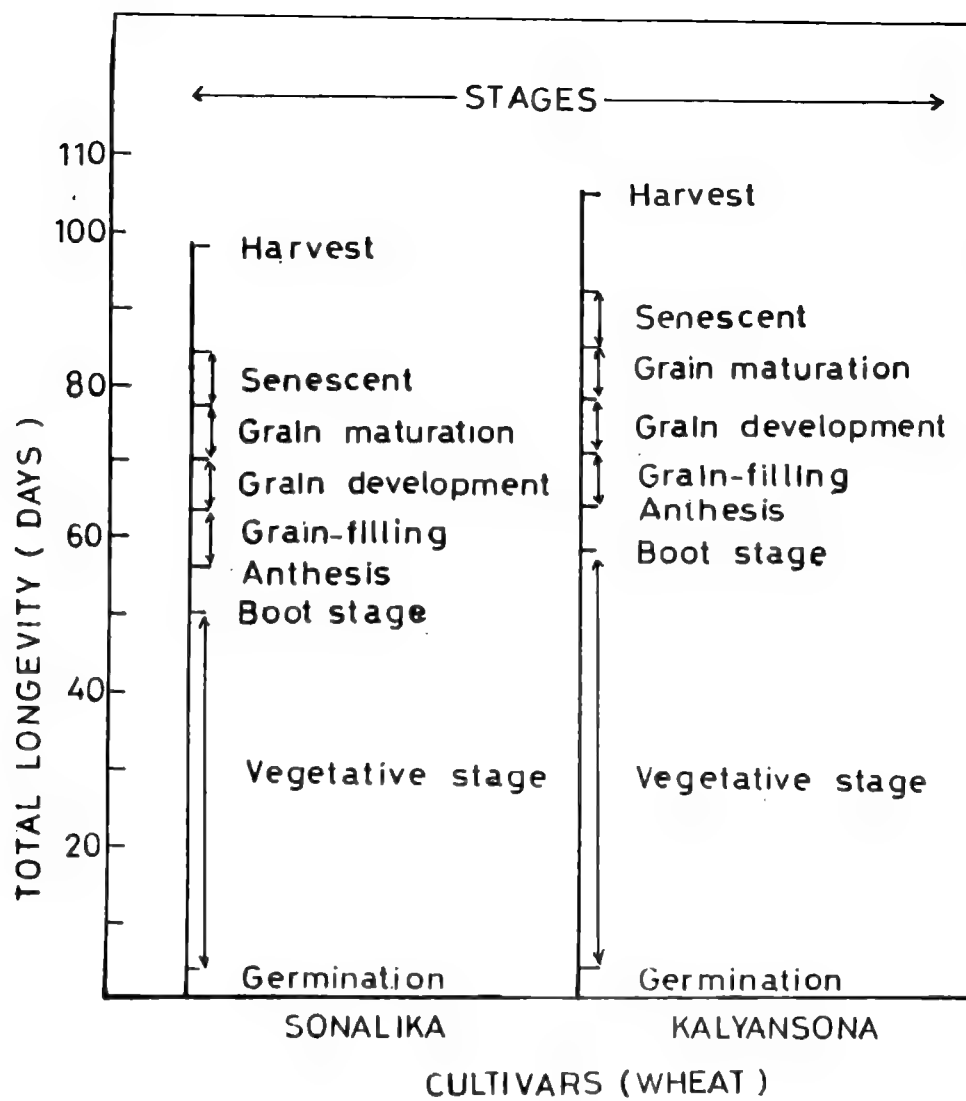
Fig. AII — Developmental stages of two wheat cultivars.

Before cultivation the soil was prepared by mixing cowdung as the only manure at the rate of 2 Kg/m$^2$ land for both the plants and watering was done at regular intervals.

### 2.2.3. Soil composition :

The average NPK composition of the soil of the cultivated land was as follows : nitrogen 0.20%, phosphorus (as $P_2O_5$) 0.047%, potassium 0.016% . The pH of the soil was around 6.4.

### 2.2.4. Design of experiments :

The following experiments were done to analyse the patterns of leaf senescence and to elucidate the possible mechanisms of monocarpic senescence in rice and wheat plants. The experimental designs are described below.

### 2.2.4.1. Study of leaf senescence behaviour of rice and wheat cultivars at the reproductive stage :

To study the leaf senescence behaviour of the flag, second and third leaf of six rice cultivars (viz., Rasi, Sashyasri, Kalojira, Badsabhog, Patnai and Kalma) and two wheat cultivars (viz., Sonalika and Kalyansona), the changes in chlorophyll and protein contents were measured at intervals of 7 days starting from anthesis (O DAA) up to the senescent stage (28 DAA). In most of the senescence experiments reported here, decline in chlorophyll and protein was taken as indicator of leaf senescence (32).

The leaf senescence patterns were also studied by considering total leaf area and percentage of yellow patches of total leaf area. The changes in nitrogen and phosphorus contents were also measured in the flag, second and third leaf of Rasi, Kalojira and Patnai rice and Sonalika wheat cultivars at intervals of 7 days during reproductive development. To elucidate the relationship with sink strength and nutrient mobilization, the total panicle weight was measured in different rice and wheat cultivars.

### 2.2.4.1.2. Assessment of $[^{32}P]$-phosphate retention and mobilization from the leaves to grains of three rice and one wheat cultivars :

To study the role of nutrient mobilization in leaf senescence behaviour, the pattern of retention and mobilization of $[^{32}P]$-phosphate from the flag, second and third leaf to the grains was studied at intervals of 7 days, starting from anthesis (0 DAA) upto the senescent stage (28 DAA), during reproductive development of three rice (viz. Rasi, Kalojira and Patnai) and one wheat (Sonalika) cultivars.

### 2.2.4.1.3. Assessment of $[^{32}P]$-phosphate mobilization patterns from roots to the flag, second and third leaf and grains during reproductive development of rice and wheat cultivars :

To elucidate the role of xylem flux containing nutrients and hormones from the roots to the vegetative and reproductive

parts in leaf senescence behaviour, the mobilization patterns of $[^{32}P]$-phosphate from roots to the flag, second and third leaf and to the grains was analysed at intervals of 7 days, starting from anthesis (O DAA) up to the senescent stage (28 DAA), during reproductive development of the above-mentioned three rice and one wheat cultivars.

### 2.2.4.1.4. Study of correlation of senescence patterns with xylem parameters at the juncture of leaf lamina and leaf sheath :

To study the correlation of senescence pattern with the xylem parameters the number of vascular bundles at the juncture of leaf lamina and leaf sheath, area of vessels in a bundle and the area of the lumen of largest vessel were recorded in three rice and one wheat cultivars.

### 2.2.4.2. Effects of hormones on the patterns of leaf senescence in rice and wheat cultivars during reproductive development :

The role of hormones on the regulation of monocarpic senescence and their effects on modification of leaf senescence behaviour were observed in two rice (Rasi and Kalojira) and one wheat cultivars (Sonalika). Rice and wheat cultivars were grown in the field and divided into 5 blocks for each culti-var. Four such blocks were used for treatments and the remaining one served as control. Benzyladenine (BA, $4.4 \times 10^{-4}$ M), gibberellic acid (GA$_3$, $2.9 \times 10^{-4}$ M), abscisic acid

(ABA, 7.5 x $10^{-5}$ M) and a combination of (BA + GA$_3$) (4.4 x $10^{-4}$M and 2.9 x $10^{-4}$ M) were separately sprayed foliarly at intervals of 7 days  on the rice and wheat cultivars in their stipulated blocks during their reproductive development, starting from the anthesis stage.

**2.2.4.2.1.** Effects of hormones on chlorophyll and protein contents in the leaves during the progress of reproductive development of rice and wheat cultivars :

Effects of the above hormones were studied on the modification of leaf senescence behaviour in terms of decline in chlorophyll and protein level in the flag, second and third leaf during reproductive development of rice and wheat cultivars at intervals of 7 days starting from the grain-filling (7 DAA) to the senescent stage (28 DAA).

**2.2.4.2.2.** Effects of hormones on nitrogen and phosphorus contents in the leaves during the progress of reproductive development of rice and wheat cultivars:

Effects of above hormones on the changes in nitrogen and phosphorus contents in the flag, second and third leaf of the above mentioned rice and wheat cultivars were studied at intervals of 7 days during their reproductive development, starting from the grain-filling (7 DAA) up to the senescent stage (28 DAA).

2.2.4.2.3. <u>Effects of BA and ABA on retention and mobiliza-</u>
<u>tion of [$^{32}$P]-phosphate from different leaves to</u>
<u>the seeds during reproductive development of rice</u>
<u>and wheat cultivars</u> :

The retention capacity of [$^{32}$P]-phosphate in the flag,
second and third leaf and mobilization from each leaf to the
developing seeds were recorded at intervals of 7 days in un-
treated control and treated rice and wheat cultivars during
their reproductive development, starting from the grain-filling
(7 DAA) to the senescent stage (28 DAA).

2.2.4.3. <u>Certain biochemical and enzymatical changes associated</u>
<u>with leaf senescence during reproductive development of</u>
<u>rice and wheat cultivars and effects of hormones on them</u>:

Rice (cv. Rasi and Kalojira) and wheat (cv. Sonalika) plants
were cultivated in the field and divided into 3 separate blocks
for each cultivar and BA and ABA were foliarly sprayed in the
respective blocks of each cultivar as described in the experi-
ment 2.2.4.2. The changes in RNA, histone protein, total free
amino acids and malondialdehyde contents and activities ef a
few enzymes generally associated with cellular degradation
and free radical metabolism (viz. protease, catalase, peroxi-
dase and superoxide dismutase) were observed at intervals of
7 days in the control and treated rice and wheat cultivars
during their reproductive development, starting from the grain-
filling (7 DAA) up to the senescent stage (28 DAA).

## 2.2.4.4. Changes in the transpiration rate and proline accumulation during reproductive development of rice and wheat cultivars and effects of hormones (BA and ABA) on them :

It is well known that hormones regulate senescence by stomatal movement which further affects the distribution of nutrients and hormones from the roots to the aerial parts. Again, stress-induced proline accumulation affects stomatal movement. Thus, in the present study the rate of transpiration and proline accumulation and effects of benzyladenine (BA) and abscisic acid (ABA) on them were studied in rice and wheat cultivars.

Rice (cv. Rasi and Kalojira) and wheat (cv. Sonalika) plants were grown in the field and divided into 3 blocks for each cultivar. Two such blocks were used for treatments and the remaining one served as control. BA ($4.4 \times 10^{-4}$ M) and ABA ($7.5 \times 10^{-5}$ M) were separately sprayed foliarly as done in the previous experiment. The changes in the rate of transpiration by the whole plant (main tiller) and by each leaf (flag, second, third) and proline accumulation in the flag, second and third leaf were recorded at intervals of 7 days during the reproductive development of above mentioned control and treated rice and wheat cultivars, starting from the grain-filling up to the senescent stage. The leaves were smeared with vaseline on both sides except the desired leaf and the rate of transpiration from this leaf was calculated.

**2.2.4.5.** <u>Changes in the endogenous level of cytokinin-like</u>
<u>substances (CK), abscisic acid and ethylene in the</u>
<u>leaves of rice and wheat cultivars during reproduc-</u>
<u>tive development</u> :

Changes in the endogenous level of CK-like substances,
abscisic acid and ethylene evolution were recorded in the flag,
second and third leaf, at intervals of 7 days during the repro-
ductive development of rice (cv. Rasi and Kalojira) and wheat
(cv. Sonalika) plants, starting from the anthesis (O DAA) up
to the senescent stage (28 DAA).

**2.2.4.6.** <u>Changes in the protein, nucleic acids (RNA, DNA) and</u>
<u>histone protein contents in the shoot apex during</u>
<u>transition from vegetative to reproductive stage of</u>
<u>rice and wheat cultivars</u> :

To partially assess changes in the genetic materials such
as histone protein, nucleic acids and total protein in the
shoot apex (which is subsequently transformed into reproductive
axis) these components were analysed in the shoot apex. The
shoot apices were collected from the different aged rice
(cv. Rasi and Kalojira) and wheat (cv. Sonalika) cultivars
18-24 days before panicle emergence, at intervals of 2 days
till the advent of panicle emergence. Collections of shoot
apices were made at the plant age starting from 71 and 94
days up to 86 and 106 days for Rasi and Kalojira rice cultivars,
respectively, and from 38 days up to 53 days for Sonalika wheat
cultivar.

**2.2.4.7.** <u>Experiments with surgically altered rice and wheat cultivars</u> :

Analyses of the mechanism of monocarpic senescence and the correlative control and effects of one organ on the other was done by surgical treatments of the plants. Thus, different $d$: surgically manipulative experiments were carried out on rice and wheat cultivars to elucidate the mechanism of monocarpic senescence. The surgical experiments undertaken for this purpose are described below.

**2.2.4.7.1.** <u>Effect of panicle removal at different stages of reproductive development of rice and wheat cultivars</u>:

The experiment was performed to analyse the role played by the leaves on whole plant senescence through mobilization of metabolites and which stage of reproductive development is most susceptible for initiating senescence. The role of panicles at different reproductive stages on senescence was also studied.

The rice and wheat cultivars grown in the field were divided into 5 blocks for each cultivar. The panicles were excised at the anthesis stage (O DAA), grain-filling stage (7 DAA), grain-development stage (14 DAA) and grain maturation stage (21 DAA) from the respective blocks of both rice and wheat cultivars. The remaining block with plants containing intact panicles served as control. The following changes in control and surgically treated cultivars were observed.

**2.2.4.7.1.1.** <u>Study of leaf senescence behaviour of the flag,</u>
<u>second and third leaf of control and surgically</u>
<u>treated rice and wheat cultivars</u> :

The leaf senescence behaviour of the control and treated
rice (cv. Rasi and Kalojira) and wheat (cv. Sonalika) culti-
vars from which the panicle was removed was observed in terms
of decline in chlorophyll and protein contents in the flag,
second and third leaf throughout the reproductive development,
starting from the anthesis (O DAA) up to the senescent stage
(28 DAA).

**2.2.4.7.1.2.** <u>Study of glume senescence in rice and wheat</u>
<u>cultivars</u> :

It was observed in the above experiments that the delaying
effect of the removal of panicle on the leaf senescence was
significantly less pronounced in wheat than in rice cultivars.
So, it was thought worthwhile to study the senescence behavi-
our of the glumes which are secondary source of photosynthate
in cereals. This study might reveal the relative contribution
of photosynthate by the reproductive structures associated
with photosynthesis. Hence, the decline in chlorophyll and
protein in the glumes of intact rice and wheat cultivars
during reproductive development was studied.

**2.2.4.7.1.3.** <u>Changes in nitrogen and phosphorus contents in</u>
<u>the leaves of control and surgically treated</u>
<u>rice and wheat cultivars :</u>

Effect of panicle removal at different reproductive stages
(0, 7, 14 and 21 DAA) on changes in nitrogen and phosphorus
contents in the flag, second and third leaf were observed and
recorded in both rice and wheat cultivars during their repro-
ductive development, at intervals of 7 days, starting from the
grain-filling (7 DAA) up to the senescent stage (28 DAA).

**2.2.4.7.1.4.** <u>Assessment of $[^{32}P]$-phosphate retention capacity</u>
<u>of each fed-leaf and of the stem (when fed</u>
<u>through flag leaf only) of control and treated</u>
<u>rice and wheat cultivars :</u>

The effect of panicle removal on $[^{32}P]$-phosphate retention
capacity of the fed flag, second and third leaf and of the
stem (when fed through flag leaf only) were observed in the
control and treated rice and wheat cultivars during their
reproductive development, at intervals of 7 days, starting
from the grain-filling stage (7 DAA) up to the senescent
stage (28 DAA).

**2.2.4.7.2.** <u>Effects of defoliation of a leaf (flag, second and</u>
<u>third separately) on the senescence of remaining</u>
<u>leaves of rice and wheat cultivars :</u>

To study the role played by each leaf on grain development,
which could also modify the senescence process of the remaining

leaves, and to elucidate the cause of monocarpic senescence, the following experiment was carried out. A particular leaf from the top was removed and its effect on the senescence of the remaining leaves was studied. The rice (cv. Rasi and Kalojira) and wheat (cv. Sonalika) cultivars were grown in the field and divided into 4 blocks as described earlier. From such blocks, the flag, second or third leaf was separately removed at the anthesis stage. The fourth block having intact plants served as control.

### 2.2.4.7.2.1. Studies on the leaf senescence behaviour of control and remaining leaves of surgically treated plants of rice and wheat cultivars :

Leaf senescence behaviour of the flag, second and third leaf of control and remaining leaves of the surgically treated rice and wheat plants was noted in terms of decline in chlorophyll and protein contents during reproductive development, at intervals of 7 days, starting from the grain-filling (7 DAA) up to the senescent stage (28 DAA).

### 2.2.4.7.2.2. Changes in nitrogen and phosphorus contents in the leaves of control and treated rice and wheat cultivars :

Effect of leaf removal at the anthesis stage on changes in nitrogen and phosphorus contents of the remaining attached leaves of the surgically treated plants over the flag, second and third leaf of control plants of rice and wheat cultivars

were observed and recorded at intervals of 7 days during their progress of reproductive development.

### 2.2.4.7.2.3. Effects of defoliation on mobilization of $[^{32}P]$-phosphate from the remaining leaves to grains during reproductive development of rice and wheat cultivars :

To study the role played by the three uppermost leaves in mobilization of nutrients and its influence on the whole plant senescence, the mobilization pattern of $[^{32}P]$-phosphate from the flag, second and third leaf of control plants and from the remaining leaves of surgically treated plants to the grains was observed and recorded at intervals of 7 days during reproductive development of rice and wheat cultivars, starting from the grain-filling (7 DAA) up to the senescent stage (28 DAA).

### 2.2.4.7.3. Effects of removal of different percentage of spikelet or emasculation on whole plant senescence of rice and wheat cultivars :

To study the source-sink relationship and its influence on the whole plant senescence, this experiment was carried out where 25, 50, 75 and 100 percent of the spikelets were removed manually from the panicle or emasculated by hot water treatment ($55^{\circ}C$ for 5 minutes) at the anthesis stage during reproductive development of both rice (cv. Rasi and Kalojira) and wheat (cv. Sonalika) cultivars. Intact rice and wheat

plants served as control. The development of secondary branches at the axil of second leaf of the main tiller was recorded. When the secondary branches developed and attained the anthesis stage, they were also subjected to above surgical treatments in an indentical way which led to the development of tertiary branch at the second leaf axil of secondary branch in a few cases of such treatments in the two rice cultivars and these were recorded. When such treatment was repeated in the tertiary branch, no further (i.e., quaternary) branch developed.

The seed production capacity and leaf area of the flag and second leaf of the main tiller, the secondary and tertiary branches of rice and only of the main tiller of wheat cultivar (where side branch development did not occur) were recorded.

2.2.4.7.3.1. <u>Study of leaf senescence behaviour of control and treated main tiller, secondary and tertiary branches of rice cultivars and the main tiller of wheat cultivar</u> :

The leaf senescence behaviour was observed in terms of decline in chlorophyll and protein contents of the top three leaves of control and surgically treated main tillers of rice and wheat cultivars and the two topmost leaves of the secondary and tertiary branches of rice cultivars (control and treated) during their reproductive development. Chlorophyll and protein contents were measured at intervals of 7 days during their reproductive development, each branch taken separately.

## 2.2.5. Methods

### 2.2.5.1. Measurement of leaf area and xylem parameters :

The area of the flag, second and third leaf of the expe-
rimental plants was measured by simple graphical method and
expressed as $cm^2$.

The number of vascular bundles was observed under a com-
pound microscope in hand-made cross sections. The area   of
xylem vessels and that of lumen  of the largest vessel  were
also recorded under a compound microscope after standardiza-
tion of the ocular with the help of a  stage micrometer and
the data were expressed as $\mu m^2$ .

### 2.2.5.2. Methods of feeding of $[^{32}P]$-phosphate through leaves and assessment of its retention and translocation to different parts :

In all experiments, 1 ml of  $^{32}P$ as  $H_3^{32}PO_4$ (19.19 MBq)
in  0.1 M  sodium  citrate  buffer  (pH 6.5)  was  fed
separately through the tip of flag, second and  third  leaf
by deeping 1 cm of the  tip  portion  into a  vial  con-
taining  isotope  solution  for  24 h. After  feeding,
randomized samples were collected from the individual organ
(flag, second, third leaf and grains, as  well  as stem and
branches as desired)  and  dried separately  on planchettes
under an  infra-red  lamp (Philips, India)  for  24 h. After

proper drying the radioactivity of the fed leaves and that
of the grains (or other parts if necessary) were measured
in a Geiger—Muller counting system (Model No. ECIL—GCS M-A,
India). The retention and mobilization of $[^{32}P]$-phosphate
were expressed as KBq. leaf$^{-1}$ h$^{-1}$.

### 2.2.5.3. Methods of feeding of $[^{32}P]$-phosphate through roots and assessment of translocation to different leaves and grains :

After careful washing, the total roots of rice and wheat
plants of each cultivar, the $^{32}P$ as $H_3^{32}PO_4$ (19.19 MBq) in
0.1 M sodium citrate buffer (pH 6.5) was fed for 5 h  by
deeping the roots into 10 ml isotope solution. The randomized
samples were collected separately from the flag, second and
third leaf and grains. The samples were then dried on plan-
chettes under infra-red lamp for 24 h. The radioactivity of
the samples was measured in a Geiger—Muller counting system.
The mobilized $[^{32}P]$-phosphate was expressed as KBq leaf$^{-1}$ h$^{-1}$.

### 2.2.5.4. Method of foliar spraying of hormones :

Aqueous solutions of benzyladenine (BA), abscisic acid
(ABA), gibberellic acid (GA$_3$), and a combination of (BA + GA$_3$)
were adjusted to pH 7 with 0.1(N) NaOH and foliarly sprayed
at intervals of 7 days using 0.5% Teepol as a surfactant at
the rate of 5 ml/plant in the respective block of rice and
wheat cultivars during their reproductive development starting

from the anthesis (0 DAA) up to the senescent stage (28 DAA).
Spraying was done with the help of a hand sprayer in the
morning to avoid scorching. Control plants were also sprayed
with an aqueous 0.5% Teepol solution only.

## 2.2.6. Method of estimation of biomolecules, enzymes and hormones :

### 2.2.6.1. Chlorophyll :

The chlorophyll content of leaf tissues was measured
following the method of Arnon (11). Fifty milligram leaf
tissues were homogenized in 5 ml cold methanol and centri-
fuged at 6000 rpm for 10 min and the supernatant was collected.
The pellets were subsequently washed in methanol and centri-
fuged again. Then the absorbance of the combined supernatant
was measured at 650 nm in a Spectrochem spectrophotometer
(AIMIL, Calcutta, Model No.RT-135). The chlorophyll content
was determined and expressed as $mg.g^{-1}$ fresh weight (FW).

### 2.2.6.2. Protein :

For protein estimation, chlorophyll-free leaf samples
were homogenized with 80% ethanol and centrifuged at
6000 rpm for 10 min. The pellets were then made phenol-free
by washing successively with 10% (w/v) trichloroacetic acid
(TCA), ethanol, ethanol : chloroform (3:1), ethanol:ether
(3:1) and finally with ether according to Kar and Mishra (179).

The pellets were dried and solubilized by treating with
2 ml 1.0(N) NaOH at $80^{o}$C for an hour in water bath. After
proper dilution, the protein content was measured following
the method of Lowry et al (216), by reacting with Folin-
phenol reagent. One ml of diluted extract was mixed with 1 ml
of solution  A (10% $Na_2CO_3$ in 0.05 (N) NaOH : $CuSO_4,5H_2O$:Na-K
tartrate = 20:1:1) and allowed to stand for 10 min. Then
3 ml of working Folin reagent were added to it rapidly.
The solution was kept for about 30 min and the OD value was
measured at 650 nm in a Spectrochem spectrophotometer. The
actual protein content of the leaf samples was determined
by comparing the OD value of the standard curve prepared
from bovine serum albumin (BSA, Fraction V powder, Sigma
Chemical Co.,USA) and expressed as mg.g$^{-1}$ fresh weight.

### 2.2.6.3. Nucleic acids :

Nucleic acids (DNA and RNA) were extracted from the
samples following the method of Cherry (57). RNA was esti-
mated according to Markham (233) by orcinol réagent  as
modified by Choudhuri and Chatterjee (62). Three ml of the
extracted solution (diluted) was mixed with 3 ml of orcinol
reagent (1 g orcinol in 100 ml conc. HCl (AR) containing
0.1% $FeCl_3,6H_2O$). After proper mixing the solution was
heated in water bath at $100^{o}$C for 20 min with glass marble
at the top of each test tube to prevent splashing. The
solutions were then cooled at room temperature and the

intensity of green colour was measured at 700 nm in a
Spectrochem spectrophotometer. Also the intensity of blank
set was measured containing 3 ml distilled water instead
of plant extract and the sample reading was corrected. The
actual RNA content was calculated by comparing the OD value
of the standard curve prepared from yeast RNA (Type II,
Biochemical Unit, V.P. Chest Institute, India) and the value
was expressed as $mg.g^{-1}$ fresh weight.

The DNA content of the samples was measured by following
the method of Burton (49). One ml of extracted DNA was mixed
with 5 ml diphenylamine reagent (1 gm of diphenylamine in
100 ml glacial acetic acid (AR, BDH), containing 2.75 ml
concentrated AR $H_2SO_4$). The solution was then heated in a
waterbath for 1 h at $100^{\circ}C$ with glass marble at the top of
each test tube. After heating, the solution was cooled to
room temperature and the intensity of blue colour developed
was measured at 600 nm in a Spectrochem spectrophotometer
deducting the blank reading done in an identical manner, but
with $H_2O$ instead of sample. DNA content was calculated by
comparing the OD value of the standard curve prepared from
herring sperm DNA (Sigma Chemical Co.) and expressed as
$mg.g^{-1}$ fresh weight.

### 2.2.6.4. Histone protein :

Histone protein was extracted following the method of
Gornall et al.(129). Leaf samples (1 gm) were homogenized

in cold 8 ml 0.3(N) HCl. The extract was centrifuged at
8000 rpm for 10 min. The residue was again extracted. After
centrifugation the supernatant was mixed with solid TCA to a
final concentration of 20% for precipitation of protein frac-
tion. The precipitation was then washed with acetone contain-
ing 1.0% HCl and followed by pure acetone only and air-dried.
Finally, the precipitate was dissolved in a fixed volume of
distilled water and the histone protein content was measured
by Folin-phenol reagent according to the method already des-
cribed and expressed as $mg.g^{-1}$ fresh weight.

## 2.2.6.5. Free amino acid :

The extraction of free amino acids was done following the
method of Dwivedi et al.(93). The leaf samples (100 mg) were
homogenized with 8 ml 80% ethanol and kept for 15 min at $60^{\circ}$C.
The solution was then centrifuged at 6000 rpm for 10 min. The
supernatant was taken in glass Petridishes and dried on a hot
plate. The chlorophyll was then removed by rinsing thrice
with 5 ml ether. To this 5 ml of 80% ethanol were then added
to the Petridish and stirred well. The extract was then used
for the estimation of total free amino acids following the
method of Moore and Stein (262). One ml of the extract was
mixed with 3 ml of 0.1% ninhydrin solution (in 80% ethanol)
in a test tube and heated in a waterbath at $100^{\circ}$C for 15 min
with a glass marble at the top to avoid splashing. The solu-
tion was then cooled to room temperature and the volume was

adjusted to 4 ml. The intensity of the purple colour deve-
loped was measured at 480 nm in a Spectrochem spectrophoto-
meter. The quantity of total free amino acids was measured
by comparing with the OD value of a standard curve prepared
from glycine (Sigma Chemical Co.) and expressed as $mg.g^{-1}$
fresh weight.

2.2.6.6. <u>Proline</u> :

The proline content of the leaf samples was measured accord-
ing to Bates et al.(19). Leaf samples were homogenized with
6 ml of 3% sulfosalycylic acid and centrifuged at 6000 rpm
for 10 min. Two ml of the extract were then mixed with 2 ml
of acid ninhydrin solution (1.25 gm ninhydrin in 30 ml glacial
acetic acid + 20 ml of 6 M orthophosphoric acid + 5 ml dis-
tilled water). The mixture was heated in a water bath at
$100^{\circ}C$ for 1 h. After heating, the mixture was kept overnight
inside the ice-chamber. The proline was separated from the
mixture by 4 ml of toluene with the help of a separating
funnel. The intensity of yellow-orange colour was measured
at 520 nm in a Spectrochem spectrophotometer. The actual
value of proline was estimated by comparing with the OD value
of a standard curve prepared from proline (Sigma Chemical Co.)
and expressed as $ng.g^{-1}$ fresh weight.

2.2.6.7. <u>Nitrogen</u> :

Nitrogen content of the leaf samples was measured follow-
ing the method of Vogel (428). Dried leaf samples were

digested in 2 ml of conc. $H_2SO_4$ (AR) for 1 h. After diges-
tion, a few drops of hydrogen peroxide ($H_2O_2$) were added
and heated until the colour of the solution disappeared.
The volume of the sample was made up to 50 ml by adding
distilled water. One ml of this extract was mixed with 1 ml
of a mixture of 10% sodium hydroxide and 10% sodium silicate
(1:1) and finally with 5 ml of Nessler's reagent ($K_2HgI_4$).
After 15 min the intensity of yellow colour was measured at
410 nm in a Spectrochem spectrophotometer. Similarly, a
blank set was made containing 1 ml of distilled water instead
of extract. The nitrogen content was determined by comparing
with the OD value of a standard curve prepared with $(NH_4)_2SO_4$
and expressed as $mg.g^{-1}$ dry weight.

## 2.2.6.8. Phosphorus :

The ash obtained from 1 gm dried leaf samples was dissolved
in 2 ml of conc. $H_2SO_4$ (AR). Then the solution was diluted up
to 100 ml and filtered through a Whatman No.1 filter paper.
Three ml of the filtrate were mixed with 1 ml of freshly
prepared chromogenic reagent for inorganic phosphorus deter-
mination following the method of Jaffe and Galston (166).
The mixture was then incubated for 15 min at $30^{\circ}C$ and the
intensity of the blue colour developed after reaction was
measured immediately at 650 nm in a Spectrochem spectrophoto-
meter. A blank was similarly prepared by adding 3 ml of
distilled water instead of extract. The value of phosphorus

was determined from a standard curve prepared by $Na_3PO_4.12H_2O$
(AR) and the phosphorus content was expressed as $mg.g^{-1}$ dry
weight.

### 2.2.6.9. Measurement of malondialdehyde (index of membrane lipid peroxidation) :

Malondialdehyde is a decomposition product of the oxida-
tion of polyunsaturated fatty acids of the biomembrane. This
was estimated following the method of Heath and Packer (148).
Five hundred mg deaf samples were homogenized in 5 ml of 1%
TCA and then centrifuged at 10,000 rpm for 10 min. One ml of
the supernatant was mixed with 3 ml of 5% TCA containing 1%
thiobarbituric acid (TBA, Sigma Chemical Co.). The mixture
was then heated in a boiling water bath for about 30 min and
then quickly cooled in an ice-bath. The solution was centri-
fuged at 10,000 rpm for 10 min and the absorbance was read at
530 nm in a Spectrochem spectrophotometer. The unspecific
turbidity was corrected by substracting $A_{600}$ from $A_{530}$ .
The quantity of malondialdehyde was measured from its extinc-
tion coefficient of 155 m $M^{-1}$ $cm^{-1}$ (148).

### 2.2.6.10. Extraction and assay of enzymes :

### 2.2.6.10.1. Catalase (EC 1.11.1.6) :

Catalase activity was measured according to the method
of Chance and Maehly (54) as described by Snell and Snell
(387). The enzyme was extracted from 200 mg leaf samples by

homogenizing with 6 ml of 0.1 M Na-phosphate buffer (pH 6.8)
in an ice-cold condition. The homogenate was centrifuged at
10,000 rpm for 10 min in a cold centrifuge ($0^{o}$C). The super-
natant was used as an enzyme source.

The activity was measured by reacting 1 ml of extract
with 2 ml of 0.0025 M $H_2O_2$ for 10 min at $37^{o}$C in an incubator.
The reaction was stopped by adding 1 ml of 1% Titanic sulphate
in 25% $H_2SO_4$ (v/v) and the mixture was centrifuged at 6000 rpm
for 15 min. The intensity of yellow colour was measured at
410 nm in a Spectrochem spectrophotometer.

## 2.2.6.10.2. Peroxidase (EC 1.11.1.7) :

Two hundred mg leaf samples were homogenized with 10 ml
of 0.1 M Na-phosphate buffer (pH 6.8) in an ice-cold condition
and centrifuged in cold condition at 17,000 rpm for 15 min.
The supernatant was then used as an enzyme source.

The enzyme activity was measured following the method of
Kar and Mishra (179). One ml of diluted enzyme extract was
mixed with the following solutions : 1.5 ml of 125 μmole
phosphate buffer (pH 6.8), 1 ml 15 μmole pyrogallol, 1 ml
50 μmole $H_2O_2$ and 0.5 ml distilled water. The reaction mixture was
then incubated for 15 min at $25^{o}$C. After incubation the reac-
tion was stopped by adding 0.5 ml of 5% $H_2SO_4$. The amount of
purpurogallin formed was determined by measuring the absorbance
at 420 nm in a Spectrochem spectrophotometer. A blank set was
similarly prepared where 1 ml distilled water was added ins-
tead of enzyme source.

### 2.2.6.10.3. <u>Superoxide dismutase</u> (SOD, EC 1.15.1.1) :

The enzyme was extracted by homogenizing 500 mg leaf samples in 5 ml 0.1 M K-phosphate buffer (pH 7.8) containing 1% (w/v) ethylene diamine tetraacetic acid (EDTA) in an ice cold condition. The homogenate was centrifuged successively at 5000 and 13,000 rpm at $0^{0}$C for 15 min and 20 min, respectively. The supernatant was used as crude enzyme source.

The reaction mixture for this enzyme activity consists of 1 ml $Na_2CO_3$ (0.05 M), 0.5 ml 15 μ M methionine, 0.5 ml 0.1 μ M EDTA, 0.1 ml of 63 μ M nitroblue tetrazolium (NBT), 2 ml enzyme extract and 0.5 ml 1.5 μ M riboflavin. Then the mixture was incubated under white fluorescent lamp (HMT, 40 W) at the intensity 180 μ mole.m$^{-2}$ sec$^{-1}$ at $30^{0}$C for 30 min. After incubation the reaction was stopped by adding 1 ml of 0.2 M potassium cyanide (KCN). Also, a blank was prepared by adding 1 ml of KCN before incubation. The intensity of colour was recorded at 560 nm in a Spectrochem spectrophotometer.

The activity was determined by measuring its ability to inhibit photochemical reduction of NBT according to the method of Giannopolitis and Ries (124) with slight modifications (350). The reduction of NBT is inversely proportional to the enzyme activity. Thus to obtain $\triangle A$, A 560 of the particular set was deducted from A 560 of the blank set, i.e., where the enzyme was killed before incubation.

## 2.2.6.10.4. Protease (EC 3.4.4X) :

Protease activity was measured according to the method of Snell and Snell (387) as modified by Biswas and Choudhuri (30). The enzyme was extracted by homogenizing 1 gm of leaf tissue in 10 ml of 0.1 M Na-phosphate buffer (pH 6.5) in an ice-cold condition. The homogenate was then centrifuged at 10,000 rpm at $0^{\circ}$C for 15 min and the supernatant was used as crude enzyme source.

The reaction mixture for measuring protease activity consists of:1 ml enzyme extract, 0.1 ml of 0.1 M $MgSO_4$ and 1 ml bovine serum albumin (BSA, 50 µg/ml). The reaction mixture was incubated at $37^{\circ}$C for an hour and then the reaction was stopped by adding 1 ml 25% TCA. A blank set was prepared where enzyme was killed before incubation by heating. The residual protein was measured by Folin-phenol reagent according to Lowry et al.(216).

If not mentioned otherwise, in each case of enzyme assay, the zero time control was taken as blank and the activity of each enzyme was expressed as $[\Delta A \times Tv/(t \times v)]$, where, $\Delta A$ is the absorbance of the sample after incubation minus the absorbance at zero time control, Tv is the total volume of enzyme extract, t is the time (min) of incubation and v is the volume of extract taken for assay (103). The enzyme activity was expressed as enzyme unit $min^{-1}$ $g^{-1}$ fresh weight.

### 2.2.6.11. Transpiration :

The root systems of the main tiller of rice and wheat cultivars after proper washing, were introduced into a specially designed 250 ml flask (wide mouth) which was filled with water. The 2 ml oil was poured into the surface of water to check the evaporation of surface water. The total set up was weighed and allowed to stand in the laboratory under the light intensity of 200 $\mu$ mole.m$^{-2}$ sec$^{-1}$ at 25 $\pm$ 2$^{o}$C. After three hours, the total set-up was reweigh{ed. The difference between the first and the second weight gave the amount of water transpired by the plant (63). The total leaf area was measured by simple graphical method. The rate of transpiration was expressed as mg H$_2$O cm$^{-2}$ h$^{-1}$. In another experiment, the transpiration rate of a single leaf was measured by smearing both surfaces of the remaining leaves with vaseline.

### 2.2.6.12. Extraction, identification, purification and estimation of abscisic acid, cytokinin-like substances and ethylene :

### 2.2.6.12.1. Abscisic acid (ABA) :

Extraction and fractionation of ABA were done according to Wright (457). Leaf samples (80 g) were homogenized with 80% methanol (10 ml/g) and extracted at 5$^{o}$C for 24 hours. The procedure was repeated once again. Methanol was evaporated in vacuo at 40$^{o}$C. The residue was reconstituted in

40 ml of warm distilled water ($35^{\circ}$C) and the aqueous extract
was adjusted to pH 2.5 with 0.1 N HCl and the free ABA was
extracted three times with diethylether (peroxide free).
Anhydrous sodium sulphate was mixed with total ether layer
and kept for 2-3 hours for drying of aqueous layer. The
ether layer containing free ABA-like substances was dried.
The residue was than redissolved in a small volume of 80%
methanol and stored at $2^{\circ}$C until used. The layer which was
partitioned against the ether layer was then taken for the
determination of bound ABA. The pH was adjusted to 7.0 with
dilute NaOH [0.01(N)] stored at $2^{\circ}$C overnight, pH was again
adjusted to 11.0 with dilute NaOH and warmed at $65^{\circ}$C for
24 hours. After hydrolysis, the solution was rapidly cooled,
pH was adjusted to 2.5 with dilute HCl [0.01(N)].

Fractionation was done in the manner described for free
ABA. The residue was dissolved in a small volume of methanol
and stored at $2^{\circ}$C. All the above extracts were further puri-
fied on silica gel coated TLC plates.

Purification of ABA :   An aliquot of the extract containing
ABA was spotted with the help of a capillary tube on the
activated TLC plates (30 min at $100^{\circ}$C). After spotting, the
plates were developed in a mixture of isopropanol:ammonia:water
(10:1:1) and the zone on the plates corresponding to ABA
marker spot (i.e. UV fluorescent spot of authentic ABA) was
scraped off and eluted with methanol and stored at $20^{\circ}$C for

48 hours. The solution was again purified on TLC plate in the same manner. The extracted ABA was then used for gas chromatography.

Estimation of ABA by gas chromatography (GC) : The authentic ABA (as standard) and TLC purified ABA extracts were methylated by diazomethane and used for GC.

Preparation of diazomethane and methylation of samples : Diazomethane was prepared following the method of Vogel (427) as follows :

Part-A : Preparation of acetyl-methyl urea : A solution of 17.7 g of acetamide ($CH_3CONH_2$) in 9 ml liquid bromine was taken in a beaker and 12 g of sodium hydroxide (NaOH) in 48 ml distilled water was added dropwise with hand stirring placing the beaker on a steam bath for dissolution of acetamide. But care was taken to minimize the loss of bromine due to heating.

The resulting mixture (yellow in colour) was heated on the steam bath until effervesence set in. The heating was permitted for additional 3 min. Crystallization of acetyl-methyl urea was obtained from the yellow to red colour solution. The crystalization was completed by cooling the reaction mixture in an ice-bath for an hour. Finally, the acetyl-methyl urea was obtained by filtration and air-drying.

**Part-B** : <u>Preparation of nitrosomethyl urea</u> : A mixture of
12 g of acetylmethyl urea and 12 ml concentrated HCl (AR)
were heated with hand stirring until the solid acetylmethyl
urea was dissolved. Heating was continued for an additional
2-3 min. And the resulting solution was diluted with an
equal volume of distilled water and cooled below $0^{o}$C in an
ice-bath. A cold sodium nitrite solution (38 g in 55 ml water)
was added to the above solution slowly with stirring. The
reaction was completed on an ice-bath for several minutes
for precipitation. The precipitate of N-nitro-N-nitroso-methyl
urea was filtered and washed with 8-10 ml of ice cold distilled
water.

**Part-C** : <u>Formation of diazomethane</u> : In an Erlenmeyer's
flask, 3 ml of 50% potassium hydroxide (KOH) and 10 ml diethyl
ether were taken and cooled in a freezing mixture. Nitroso-
methyl urea (1 g) was then added to the cold solution in small
portion with shaking. The layer turned yellow due to formation
of diazomethane. The aqueous layer was separated from the
non-aqueous layer and washed with ice-cold water.

**Part-D** : <u>Methylation (esterification) of samples</u> : Methyla-
tion of authentic ABA and extracted ABA was done according
to Ross and Bradbeer (349). One ml of precooled ether solution
of extracted ABA was treated with 10 ml of diazomethane for
10 min. Solid ester of ABA separated out as precipitate.

The excess solution was evaporated at room temperature
$(25 \pm 2^{o}C)$ and then used for GC.

Samples were then identified and estimated by GC using
the methyl ester of both extracted and authentic ABA (441).
The cis-trans ABA (Sigma Chemical Co.) was used as authentic
sample. The methyl esters were dissolved in a small volume
of methanol and 5 µl of the solution was used for GC in Pye
Unicam GC (Pye series 104) fitted with flame ionising detec-
tor device. The GC was done at the Bose Institute, Calcutta.
The glass column (length 125 cm, internal diameter 1/4 cm)
was packed with 5% SE-30 coated on 80-100 mesh acid washed
and AW-DMCS treated chromosorb W. The column was precondi-
tioned overnight at $300^{o}C$. Injector and detector temperatures
were maintained at $190^{o}C$ and $212^{o}C$, respectively. The nitrogen
gas flow rate was 40 ml/min (used as a carrier gas). The
amount of ABA present in the sample was determined by com-
paring the peak area percentage with the standard.

## 2.2.6.12.2. Cytokinin-like substances :

Fresh 70 g leaf samples were homogenized with 80% methanol
(10 ml/g) and cytokinin-like substances were extracted follow-
ing the method of Obata-Sasamoto and Suzuki (301). The
extract was kept at $3^{o}C$ for 24 hours. The methanol was
filtered and the residue was extracted again with methanol.
Pooled methanol was centrifuged at 15,000 rpm for 10 min and

the supernatant was evaporated in vacuo at $30^{o}C$. The pH
of the aqueous phase was adjusted to 2.5 with 1 N HCl and
washed 3 times, each time with 1/3 volume of methylene
chloride. The aqueous phase again adjusted to pH 8 with 5%
$NaHCO_3$ and extracted with 1/3 volume of water-saturated
butanol. The extraction was repeated thrice. The pooled
butanol was evaporated in vacuo at $28 \pm 3^{o}C$. The résidue
was dissolved in 0.5 ml NaOH (0.05 N) and used for further
purification chromatographically (TLC).

Purification of cytokinin-like substances : The extracted
cytokinin-like substances (CK) were spotted on TLC plates
(activated) along with authentic samples. The plates were
then developed in solvent system (n-butanol:acetic acid:water
= 4:1:1). The plates were then observed under UV lamp and
all the fluorescent spots of authentic and extracted samples
were marked. The Rf zones equivalent to authentic samples
were scraped off from the TLC plates and eluted thrice with
80% methanol keeping at $5^{o}C$ for 12 h. The extract was then
used for determination of biological activity.

Bioassay of extracted CK-like substances : The cytokinin-
induced chlorophyll formation in cucumber cotyledons (106)
was used for testing the biological activity and estimation
of CK-like substances of the extracted samples. The cucumber
seeds (Cucumis sativa cv. Long green) were germinated in the

dark at 26 $\pm$ 2$^o$C for 4 days. The cotyledons were excised
and placed in a small Petridish (2'' diameter) containing
3 ml of test solution. The Petridishes were first incubated
in darkness for 14 h (26 $\pm$ 2$^o$C) and then placed under the
fluorescent lamp (20 $\mu$ mol.m$^{-2}$ sec$^{-1}$). The above experiment
was repeated with 3 ml of kinetin solution (used as a stan-
dard), concentration ranging from 0.001 to 0.1 mg.lit$^{-1}$
which gave a linear response (106). After 24 h the chloro-
phyll of the cotyledons  was extracted in methanol (10 ml)
and the chlorophyll concentration was estimated ( II  )                 .
By comparing the absorbancy of the chlorophyll induced by the
authentic cytokinin (  kinetin), the amount of CK-like subs-
tances in the extract was determined.


## 2.2.6.12.3. Ethylene :

The evolution of ethylene was measured colorimetrically
following the method of LaRue and Kurz (200) with slight
modifications. Five hundred mg leaf samples were taken in a
well stoppered vial, and to it 1.5 ml of oxidant solution
(50 ml 0.05 M NaIO$_4$ + 10 ml of 0.005 M KMnO$_4$, pH 7.5) was
injected. The vial was made partial air free with the help
of a syringe and agitated vigorously on a rotary shaker
for about 3 h at room temperature. Then 0.25 ml of 4 N
sodium arsenate and 0.25 ml of 4 N H$_2$SO$_4$ were added to the
vial to destroy the excess oxidant. One ml of Nash reagent

(150 gm of ammonium acetate + 3 ml acetic acid + 2 ml acetyl-
acetone, diluted up to a liter) was added with the above
solution. After one hour, a yellow colojration appeared and
the absorbance was measured at 412 nm in a Spectrochem spec-
trophotometer. In the same way, a standard curve was prepared
with ethrel.

The content of ethylene in the ethrel was determined by
gas        chromatography (Column 'Porapack N', oven tempera-
ture 80°C, detector and injector temperature 100°C, nitrogen
used as the carrier gas, flow rate 40 ml/min. This was done
at the Botany Department, Kalyani University, West Bengal
through courtesy of Prof.S.P.Sen). One ml of concentrated
ethrel contained 1.6207 ml ethylene gas. The amount of ethy-
lene released by the sample was determined by comparing it
with the standard curve of ethrel (where ethylene content
was already been measured by GC).

## 2.2.7. Statistics :

The field experiments were repeated thrice, i.e., in
a particular season of three different years. Biochemical
parameters were analysed by taking six replications in
each set of experiments and the data were incorporated in
tables and figures.

The data included in tables were statistically analysed for LSD values at 95% confidence limits at the treatment and replication levels (314). The data which are presented in percentage were transformed into angular variances [$sin^{-1}$ transformation of Fisher and Yates (105)] and the statistical representations were made according to the above method. The standard errors around the mean were calculated (67) and plotted in figures.

# R E S U L T S

## 2.3.1. <u>Study of the pattern of leaf senescence of six rice and two wheat cultivars</u> :

2.3.1.1. Study of the pattern of leaf senescence in terms of chlorophyll and protein contents and percentage of yellowing patches of total leaf :

The leaf senescence behaviour of the flag, second and third leaf of six rice and two wheat cultivars was studied in terms of decline in chlorophyll and protein contents with the progress of reproductive development and the results have been presented in Figures 1 to 3. The chlorophyll and protein contents of the flag, second and third leaf gradually decreased in all the rice and wheat cultivars. In short-statured Rasi and Sashyasri rice cultivars, the levels of chlorophyll (Figure 1)and protein (Figure 2) were greater in the flag leaf than in the second and third leaf until the grain maturation stage (21 DAA) , but at the senescent stage (28 DAA) the reverse trend was noted,   where the levels of above components were greater in the older second leaf than in the younger flag leaf. On the other hand, in medium-statured Kalojira and Badsabhog rice cultivars, the loss of chlorophyll (Figure 1)

and protein (Figure 2) of the leaves was related to the chro-
nological age of the leaf i.e., the flag leaf always contained
greater level of chlorophyll and protein than the older second
and third leaf throughout the reproductive development. How-
ever, in the tall Patnai and Kalma rice cultivars, the flag
leaf contained higher levels of chlorophyll and protein than
the second leaf up to the grain maturation stage but at the
senescent stage the loss of above substances was more exten-
sive in the flag than in the second leaf and their levels be-
come almost equal in both flag and the second leaf at the
senescent stage. As in medium-statured rice cultivars, in
Sonalika and Kalyansona wheat cultivars, the loss of chloro-
phyll and protein (Figure 3) was related to the chronological
age of the leaf and their levels were always higher in the
younger flag leaf than in the more aged second and third leaf.
In all the rice and wheat cultivars, the degradation of chlo-
rophyll and protein was most extensive in the third leaf.

It was observed (Figures 4 & 5) that the area of second
leaf of Rasi and Sashyasri rice cultivars was almost double
that of the flag leaf, whilst this was almost equal in the
two uppermost leaves of medium-statured Kalojira and
Badsabhog rice cultivars. But in the tall Kalma and Patnai
rice cultivars the area of the second leaf was slightly
larger than that of the flag leaf. As in Patnai and Kalma,
the area of the second leaf in Sonalika and Kalyansona

wheat cultivars was slightly greater than that of the flag
leaf (Figures 6 & 7). It was observed that the onset of
senescence or yellowing started earlier in the second leaf
than in the flag leaf in all the rice and wheat cultivars
(Figures 4 & 6). The yellowing patches of the flag leaf of
Rasi and Sashyasri cultivars remained smaller than that of
the second leaf up to the grain maturation stage (21 DAA),
but an opposite picture was observed at the senescent stage
(28 DAA, Plate 1A & B). In medium-statured Kalojira and
Badsabhog rice cultivars, these patches were greater in the
second leaf than in the flag leaf throughout the reproduc-
tive development (Plate 1C & D). Whereas, in tall Patnai and
Kalma rice cultivars, yellowing patches were greater in the
second leaf than in the flag leaf up to the grain maturation
stage (21 DAA), but these were more or less equal at the
senescent stage (28 DAA, Plate 1E & F). In Sonalika and
Kalyansona wheat cultivars (Figures 6 & 7) such development
of yellowing patches was proportional to the chronological
age of the leaves and always greater in the second leaf
than in the flag leaf throughout the reproductive deve-
lopment.

2.3.1.2. <u>Changes in the contents of nitrogen and phosphorus
in the leaves</u> :

Changes in the contents of mineral nutrients, viz.,
nitrogen and phosphorus, were measured in the flag, second

A — RASI

B — SASHYASRI

C — BADSABHOG

D — KALOJIRA
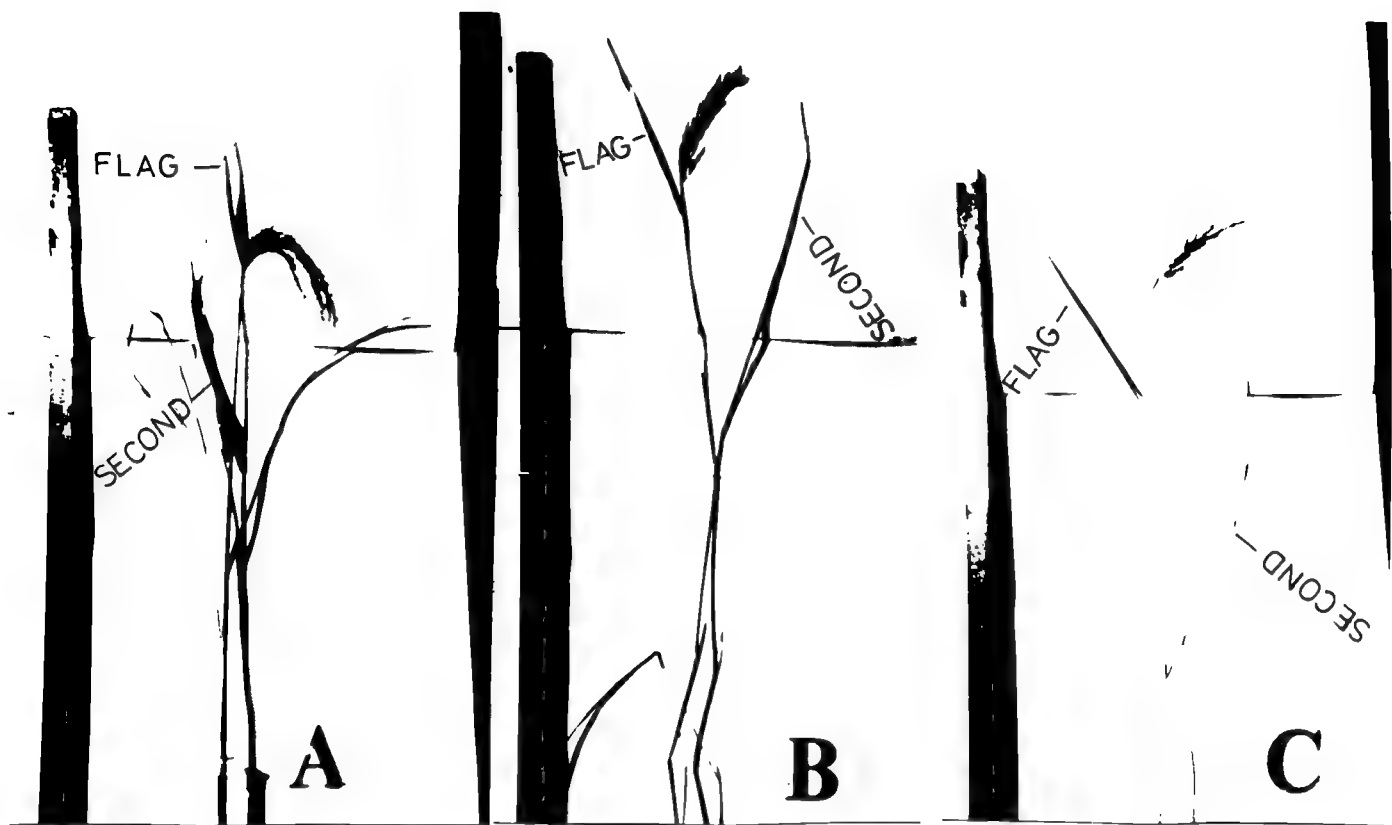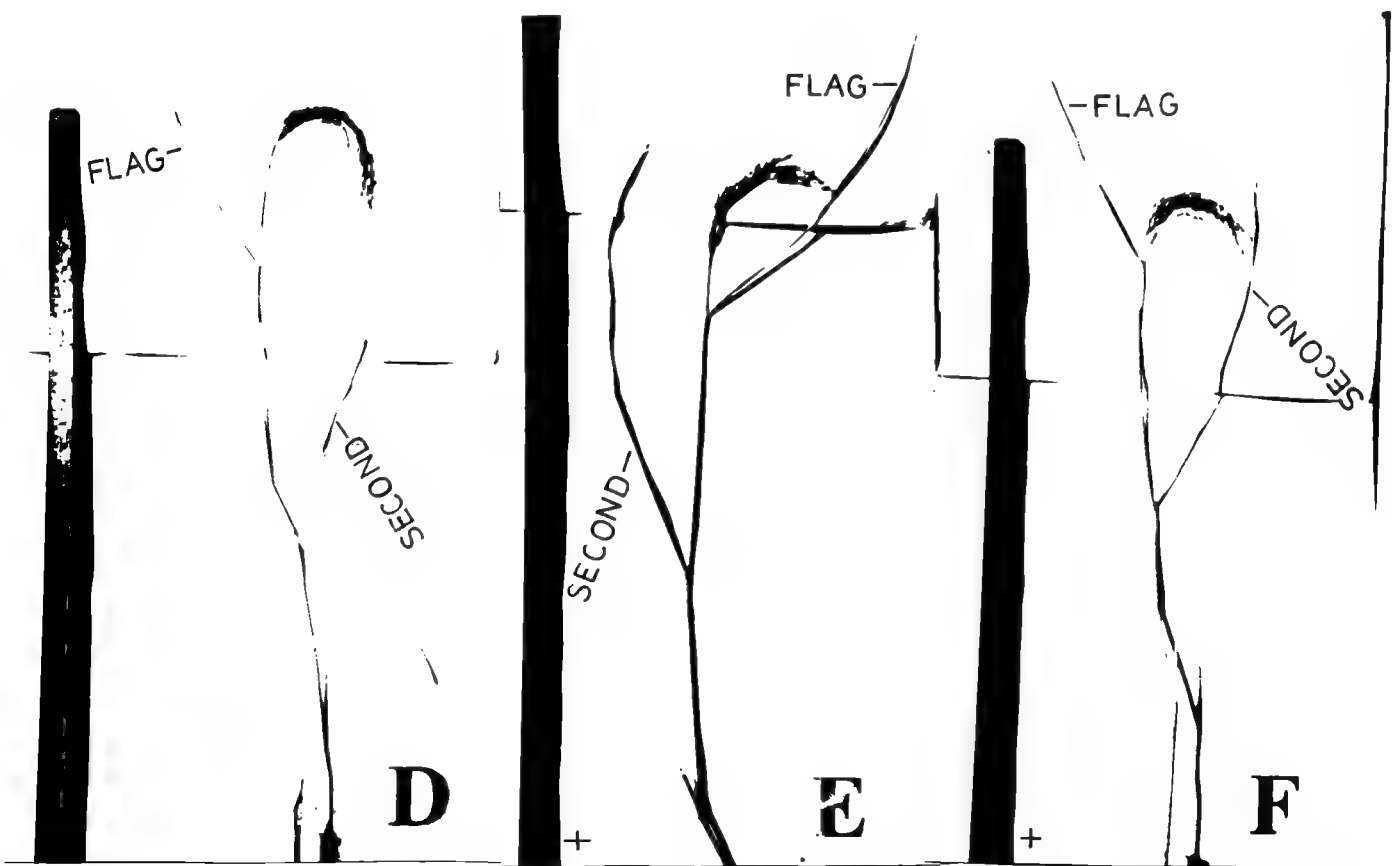
E — KALMA

F — PATNAI

## Plate 1

and third leaf of three rice and one wheat cultivars during
the progress of their reproductive development and the
results have been incorporated in Figures 8 & 9. The con-
tents of nitrogen and phosphorus in all three uppermost
leaves of rice and wheat cultivars gradually decreased
during the progress of their reproductive development, but
drastically so at the later stage (14 to 28 DAA). In Rasi,
the decline of above mineral nutrients was larger in the
flag leaf than in the second leaf at the grain maturation
(21 DAA) and senescent (28 DAA) stages. Thus, at the sene-
scent stage, their contents were greater in the second leaf
than in the flag leaf (Figures 8 & 9). Whereas, in medium-
statured Kalojira rice and Sonalika wheat cultivars, the
decline in nitrogen and phosphorus from the leaves took
place in accordance with their chronological age and more
pronounced decline was noticed in the older second leaf
than in the younger flag leaf. In tall Patnai rice cultivar,
the decline of these nutrients took place at almost equal
pace from the flag and the second leaf.

2.3.1.3. $[^{32}P]$-phosphate mobilization from leaves to grains:

The pattern of $[^{32}P]$-phosphate mobilization from (Figures
10 & 11) the flag, second and third leaf to the seeds and
their retention (Figure 12) were recorded in three rice and
one wheat cultivars during their progress of reproductive
development. The export of $[^{32}P]$-phosphate from leaves to

grains varied between species as well as among cultivars.
A greater amount of $[^{32}P]$-phosphate export was noted in
rice cultivars in comparison with the wheat cultivar.
Among the rice cultivars this was maximal in tall Patnai
followed by Kalojira and Rasi. In all the rice and wheat
cultivars, the maximal mobilization of $[^{32}P]$-phosphate to
the panicle was observed from the flag leaf and minimal
from the third leaf. The mobilization of $[^{32}P]$-phosphate
from all the leaves gradually increased reaching the maximal
level at the grain development stage (14 DAA) and declined
thereafter (Figure 10).

In Rasi, the export of $[^{32}P]$-phosphate on unit leaf
area basis, was much higher from the flag leaf than from
the second and third leaf to the grains (Figure 11). In
Kalojira, such difference in mobilization between the flag
and the second leaf was less pronounced than that observed
in Rasi. The mobilization of $[^{32}P]$-phosphate from the flag
leaf on unit leaf area basis was larger in both Kalojira
rice and Sonalika wheat cultivars. Among the rice cultivars,
the export of $[^{32}P]$-phosphate was maximal in Rasi and minimal
in tall Patnai cultivar. In Sonalika wheat cultivar, the
mobilization of $[^{32}P]$-phosphate per unit leaf area basis
was maximal from the flag and minimal from the third leaf
(Figure 11).

It was observed that $[^{32}P]$-phosphate retention capacity (per leaf basis) of the fed leaves gradually decreased during the reproductive development of rice and wheat cultivars (Figure 12). In Rasi, the retention was greater in the flag leaf than in the second leaf up to the grain development stage (14 DAA), but this was reversed at the grain maturation stage (21 DAA), being greater in the second leaf than in the flag leaf. Whereas in Kalojira rice and Sonalika wheat cultivars, the retention capacity was always greater in the flag leaf than in the second leaf throughout the reproductive development. In Patnai rice cultivar, the retention capacity was marginally greater in the flag than in the second leaf at the senescent stage (28 DAA). The pattern of retention of $[^{32}P]$-phosphate by different leaves of Kalojira rice and Sonalika wheat cultivars was identical. The isotope retention capacity was maximal in Patnai and minimal in Rasi.

The total weight of panicle was separately recorded in all the rice and wheat cultivars (Table 1). Among rice cultivars, the panicle weight was maximal in tall Patnai and minimal in short-statured Rasi rice cultivar. In both medium-statured Kalojira rice and Sonalika wheat cultivars, the panicle weight was slightly greater than that in Rasi rice cultivar.

## 2.3.1.4. $[^{32}P]$-phosphate mobilization from roots to leaves and grains :

The pattern of $[^{32}P]$-phosphate mobilization from roots to the flag, second and third leaf and to the seeds during

the progress of reproductive development of three rice and
one wheat cultivars was represented in the Figure 13. The
mobilization of $[^{32}P]$-phosphate from roots to leaves and
seeds gradually declined during progress of reproductive
development of each cultivar and this was more marked in
rice than in wheat cultivars. In Rasi, the export of
$[^{32}P]$-phosphate from roots to the second leaf remained
greater than that of the flag leaf throughout the reproduc-
tive development, whereas in Kalojira, this was significantly
greater to the flag leaf than to the second leaf at the
grain development (14 DAA) and senescent stage (28 DAA).
Among the rice cultivars, maximal export of $[^{32}P]$-phosphate
from roots to the leaves was recorded in Patnai and minimal
in Rasi rice cultivar. In Patnai, the export of $[^{32}P]$-phosphate
from roots to the second leaf was slightly larger than that
to the flag leaf until the grain maturation stage (21 DAA)
but at the senescent stage (28 DAA) it was reversed, being
marginally higher to the flag leaf than to the second leaf.
It was noticed that degree of decline of $[^{32}P]$-phosphate
mobilization from roots to leaves was greater in Patnai than
in the other two rice cultivars. In Sonalika wheat cultivar,
the mobilization of $[^{32}P]$-phosphate from roots to the flag
leaf was larger than that of the second leaf at the grain
development (14 DAA) and senescent (28 DAA) stage. In all
the rice and wheat cultivars, mobilization of $[^{32}P]$-phosphate
to the seeds gradually decreased during the progress of
reproductive development.

## 2.3.1.5. Correlation of leaf senescence patterns with xylem parameters at the juncture of leaf lamina and leaf sheath :

To elucidate the role of vascular bundles in facilitating mobilization of nutrients and hormones and its influence on nonsequential and sequential modes of leaf senescence behaviour, the number of vascular bundles at the juncture of leaf lamina and leaf sheath, area of the vessels in a bundle and the area of the lumen of the largest vessel were studied in the above rice and wheat cultivars and the results have been shown in Table 2. The number of vascular bundles, the area of xylem vessels in a bundle and the area of lumen of the largest vessel were variable among the leaves and between cultivars. These xylem parameters were greater  in the second leaf than in the flag leaf in short-statured Rasi rice cultivar. On the other hand, these were almost equal in both the flag and the second leaf of medium-statured Kalojira rice cultivar (Table 2). But in tall Patnai, the above xylem parameters were marginally greater in the second than in the flag leaf (Table 2). The total number of vascular bundles and the area of xylem vessels in a bundle of the flag and second leaf of rice cultivars have been diagramatically represented in Figure 14. In Sonalika wheat, the number of vascular bundles was more or less equal in both flag and second leaf but the area of xylem vessels in a bundle and that of the largest vessel were marginally greater in the second leaf than in the flag leaf (Table 2).

2.3.2. <u>Effects of hormones on modification of the patterns</u>
<u>of leaf senescence in rice and wheat cultivars</u>

2.3.2.1. Study of effects of hormones on modification of
the pattern of leaf senescence in rice and wheat
cultivars in terms of decline in chlorophyll and
protein :

Effect of benzyladenine (BA, $4.4 \times 10^{-4}$ M), gibberellic
acid (GA$_3$, $2.9 \times 10^{-4}$ M), abscisic acid (ABA, $7.5 \times 10^{-5}$ M)
and (BA + GA$_3$) [BA, $4.4 \times 10^{-4}$ M and GA$_3$, $2.9 \times 10^{-4}$ M) on
modification of leaf senescence behaviour of the flag, second
and third leaf of two rice and one wheat cultivars represent-
ing the nonsequential and sequential modes of senescence
(i.e., two extreme types) were studied in terms of decline
in chlorophyll and protein contents and the results have
been entered in Tables 3 to 6. BA treatment significantly
increased chlorophyl and protein level  of each leaf over
the untreated control leaves in all these rice and wheat
cultivars (Table 3). In Rasi, the application of BA mainta-
ined higher levels of chlorophyll and protein in the flag
leaf than in the second leaf until grain maturation stage
(21 DAA) but at the senescent stage (28 DAA), this was
reversed. On the other hand, in Kalojira rice and Sonalika
wheat cultivars, BA treatment maintained higher levels of
chlorophyll and protein in the flag leaf than in the second
leaf until the senescent stage. External application of GA$_3$
slightly retarded the loss of chlorophyll and protein in

all leaves of rice and wheat cultivars at all stages of
reproductive development. However, retardation caused by
$GA_3$ was significantly smaller than that by BA (Table 4).
Also, $GA_3$ application like BA did not alter the pattern of
leaf senescence of rice and wheat cultivars. ABA treatment,
in general enhanced the loss of chlorophyll and protein in
all three leaves of rice and wheat cultivars at all stages
of reproductive development (Table 5). This effect of ABA
became more prominent in the flag and second leaf during
later stages of reproductive development (21 and 28 DAA).
While in the third leaf, this became evident even at the
grain development stage (14 DAA). In Rasi rice cultivar,
ABA treatment did not alter the senescence pattern, and the
second leaf always contained greater chlorophyll and protein
than the flag leaf even at the senescent stage (28 DAA).
This trend was also noted in Kalojira rice and Sonalika
wheat cultivars, where the flag leaf always contained
higher level of the above components than the second leaf
throughout reproductive development. Treatment of leaves
with a combination of (BA + $GA_3$) greatly augmented the
chlorophyll and protein levels of three leaves in both rice
and wheat cultivars (Table 6). The effect of the combined
treatment of (BA + $GA_3$) was slightly greater than that of
BA alone in all the cultivars of rice and wheat and the
effect was most prominent at the later stages of reproduc-
tive development (14 to 28 DAA). However, above treatments
did not alter the mode of leaf senescence of any cultivar.

## 2.3.2.2. Effects of hormones on nitrogen and phosphorus contents of leaves :

Effect of foliar application of BA, $GA_3$, ABA and (BA + $GA_3$) on changes in nitrogen and phosphorus contents of the flag, second and third leaf were studied and the results have been incorporated in Tables 7 to 10. Application of BA markedly arrested the decline of nitrogen and phosphorus contents in all three leaves of rice and wheat cultivars (Table 7) and the effect became more evident after the grain development stage (14 DAA). The increase over control in the contents of these nutrients due to BA treatment was more pronounced in the flag than in the second leaf in Rasi rice cultivar, whereas in Kalojira rice and Sonalika wheat cultivars, the increase in the contents of nitrogen and phosphorus was slightly greater in the second than in the flag leaf due to BA treatment. Application of $GA_3$ also slightly inhibited the loss of nitrogen and phosphorus in all the leaves of rice and wheat cultivars. The retarding effect of BA application on nutrient loss was, however, greater than that of $GA_3$ (Table 8). Contrary to the effect of BA and $GA_3$, ABA application accelerated the loss of above nutrients from the leaves of rice and wheat cultivars at all stages of their reproductive development (Table 9), and the effect was more spectacular after grain development stage (14 DAA). It was noted that a combined treatment of (BA + $GA_3$) strongly retarded the loss of

above nutrients from the leaves in all rice and wheat cultivars (Table 10). None of the hormones, when applied alone or in combination, did alter the pattern of the loss of nitrogen and phosphorus from the leaves in both rice and wheat cultivars (Tables 7 to 10).

### 2.3.2.3. Effect of treatment of BA and ABA on $[^{32}P]$-phosphate retention by and export from leaves to grains :

BA treatment augmented translocation of $[^{32}P]$-phosphate from the flag, second and third leaf to the grains of all the rice and wheat cultivars during reproductive development (Table 11). BA strongly augmented the export of $[^{32}P]$-phosphate from the flag leaf to the seeds in all the cultivars and such export was larger from the flag than that from the second leaf. Along with the augmentation of export of $[^{32}P]$-phosphate, BA also increased the retention capacity of each of the fed leaf (flag, second and third) of all the cultivars, which became most pronounced at the later stages of reproductive development (Table 11). BA greatly increased the retention capacity of the flag leaf of Rasi rice cultivar and of the second leaf of Kalojira rice and Sonalika wheat cultivars. On the other hand, ABA treatment produced an effect opposite to that of BA, which not only reduced the export of $[^{32}P]$-phosphate but also the retention capacity of the isotope in all the rice and wheat cultivars (Table 12).

### 2.3.3. Some senescence related biochemical and enzymatical changes in the leaves during reproductive development of rice and wheat cultivars and effects of hormones on them :

Changes in the contents of RNA, histone protein and the ratio between RNA and histone in the flag, second and third leaf of two rice (Rasi and Kalojira) and one wheat cultivars (Sonalika) were recorded along with the effects of application of BA and ABA on them with the progress of reproductive development and the results have been reprcesented in Figures 15 and 16 and Table 13. The histone level gradually increased, while the RNA level and the ratio between RNA and histone gradually decreased in the flag, second and third leaf in both rice and wheat cultivars (Figures 15 & 16) and the decrease was most pronounced at the grain maturation (21 DAA) and senescent stage (28 DAA). The decrease in RNA and the ratio between RNA and histone at the senescent stage was faster in the flag leaf than in the second leaf in Rasi. Whilst in Kalojira rice and Sonalika wheat cultivars, these parameters decreased at a faster rate in the second leaf than in the flag leaf. On the other hand, histone protein content increased concemitant with the decrease in RNA content. The largest increase in histone protein was observed in the third leaf of each cultivar. Also, the maximal rise in histone protein level in each leaf was recorded at the senescent stage (28 DAA).

Foliar application of BA strongly inhibited the decrease in the RNA and the ratio between RNA and histone and increase in the histone protein content in all the leaves of rice and wheat cultivars. Such treatment also maintained a greater level of RNA and a higher ratio of RNA/histone and a lesser level of histone protein in the leaves compared with that of untreated control plants (Table 13). The marked effect of BA was observed after grain development stage (14 to 28 DAA). On the other hand, ABA treatment gave an opposite effect, i.e., strongly promoting the loss of RNA, lowering the ratio of RNA/histone and increasing histone protein level in all the leaves of rice and wheat cultivars (Table 13). Like BA, its effect was more pronounced at the later stages of reproductive development.

The accumulation of free amino acids gradually increased in the flag and second leaf up to the grain maturation stage (21 DAA) but slightly decreased at the senescent stage (28 DAA) in all the rice and wheat cultivars (Figure 17). But in the third leaf of these cultivars, such accumulation increased only up to the grain development stage (14 DAA), decreasing thereafter. However, in Sonalika wheat cultivar, the maximal accumulation of free amino acids occurred in the third leaf at the grain-filling stage (7 DAA), decreasing thereafter. In Rasi rice cultivar, the maximal accumulation of amino acids was observed in the flag leaf at the grain maturation stage (21 DAA), whereas this was maximal in the second leaf

in Kalojira rice and Sonalika wheat cultivars. Concomitant with the rise in free amino acid accumulation, the protease activity also increased gradually in all the leaves of both rice and wheat cultivars (Figure 18). The maximal increase was recorded in the third leaf at the senescent stage (28 DAA) of all the cultivars. The protease activity of the flag leaf of Rasi was greater than that of the second leaf only at the senescent stage. However, the activity of this enzyme showed an opposite trend in the flag and second leaf of Kalojira rice and Sonalika wheat cultivars, where the protease activity increased in the leaves according to the chronological age of leaves.

BA treatment significantly retarded the rise in free amino acid accumulation as well as protease activity in all the leaves of rice and wheat cultivars (Table 14). Such effect of BA was maximal at the grain maturation and senescent stage. ABA, on the contrary, markedly promoted the rise in free amino acid accumulation as well as protease activity in all the leaves of rice and wheat cultivars, but its effect was maximal at the grain maturation and senescent stage (Table 14). In both these treatments, the effect was maximal in the flag leaf of Rasi rice cultivar and in the second leaf of Kalojira rice and Sonalika wheat cultivars.

Changes in malondialdehyde (MDA) content and activities of superoxide dismutase (SOD) (Figure 19), catalase and

peroxidase (Figure 20) in the flag, second and third leaf
of two rice (Rasi and Kalojira) and one wheat (Sonalika)
cultivars were recorded during their reproductive develop-
ment. The MDA (a product of oxidation of membrane poly-
unsaturated fatty acids) content increased gradually in all
the leaves of rice and wheat cultivars, reaching a maximal
level at the grain maturation (21 DAA) and senescent stage
(28 DAA) (Figure 19). The maximal increase was noted in the
third leaf at the senescent stage of all the cultivars, and
minimal in the second and flag leaf of Rasi and Kalojira rice
cultivars, respectively. The pattern of change of MDA in
leaves of Sonalika wheat cultivar was similar to that of
Kalojira rice cultivar. The activities of SOD (Figure 19)
and catalase (Figure 20) gradually decreased in the leaves
of both rice and wheat cultivars but maximal decrease took
place in the third leaf in all these cultivars. The degree
of decrease of the above enzymes at the senescent stage was
greater in the flag leaf than in the second leaf of Rasi
rice cultivar, but this was opposite in Kalojira rice and
Sonalika wheat cultivars. On the other hand, the peroxidase
activity (Figure 20) gradually increased in the flag and the
second leaf of rice and wheat cultivars up to the grain
maturation stage (21 DAA), but decreased at the senescent
stage (28 DAA). In the third leaf of all cultivars, this
enzyme activity gradually increased up to the grain develop-
ment stage (i4 DAA), declining thereafter.

External application of BA significantly arrested MDA
production and increased the activities of SOD (Table 15),
catalase and peroxidase (Table 16) in the leaves of rice
and wheat cultivars. The effect of BA on the inhibition of
MDA production and on the promotion of the activities of SOD
(Table 15), catalase and peroxidase (Table 16) was maximal
in the flag leaf of Rasi rice cultivar and in the second
leaf of Kalojira rice and Sonalika wheat cultivars, respec-
tively. On the other hand, ABA significantly augmented MDA
production but inhibited SOD (Table 15), catalase and pero-
xidase (Table 16) activities. However, the effects of BA
and ABA on these parameters were more prominent at the later
stages of reproductive development.

2.3.4. Changes in the transpiration rate and proline accumu-
lation during reproductive development of rice and
wheat cultivars and effects of hormones on them :

Changes in the rate of transpiration and proline accumula-
tion in the flag, second and third leaf and the effect of
hormones on them during reproductive development of rice and
wheat cultivars were shown in Figure 21 and Tables 17 to 19.
The rate of transpiration was higher in Rasi    than that in
Kalojira rice cultivar and lower in wheat cultivar throughout
the reproductive development. The rate of transpiration
gradually decreased in all the rice and wheat cultivars with
the progress of reproductive development. Transpiration rate

was maximal at the anthesis stage (O DAA) and minimal at
the senescent stage (28 DAA) (Table 17). It was noted that
the rate of transpiration by a single leaf (when prevented
in other leaves by vaseline smearing) of a plant was signi-
ficantly greater than that of the whole plant. Like the
whole plant, the rate of transpiration by each leaf also
gradually decreased with the progress of reproductive deve-
lopment (Table 17). In Rasi, the rate of transpiration by
the flag leaf was greater than that by the second leaf up
to the grain maturation stage (21 DAA), but this trend was
reversed at the senescent stage (28 DAA), when the rate of
transpiration was greater in the second than in the flag
leaf. However, in Kalojira rice and Sonalika wheat cultivars,
the rate of transpiration was maximal by the flag leaf
followed by the second and third leaf throughout the repro-
ductive development (Table 17). Foliar application of BA
significantly accelerated the rate of transpiration by the
whole plant as well as by the single leaf, whilst ABA treat-
ment inhibited the same in all the rice and wheat cultivars
(Table 18). The effects of BA and ABA were most pronounced
at the laterstages of reproductive development. Such effect
was maximal in the flag leaf of Rasi rice cultivar and
second leaf of Kalojira rice and Sonalika wheat cultivars.

In contrast to transpiration rate, proline accumulation
gradually increased in the flag, second and third leaf dur-
ing reproductive development of rice and wheat cultivars

(Figure 21). In Rasi, proline accumulation increased in
the leaves according to their chronological age up to the
grain development stage (14 DAA) but this sequence was
reversed at the grain maturation stage when the flag leaf
contained the highest level of proline followed by the
second and third leaf and this sequence was maintained up
to the senescent stage (28 DAA). Unlike that in Rasi rice
cultivar, in Kalojira rice and Sonalika wheat cultivars,
the proline accumulation increased in the leaves proporti-
onal to the leaf age, i.e., higher accumulation in the older
leaf than in the younger leaves took place up to the grain
maturation stage (21 DAA) of the reproductive development.

Foliar application of BA significantly suppressed pro-
line accumulation in all the leaves of rice and wheat cul-
tivars throughout the reproductive development (Table 19).
The effect of BA on the above parameter was most pronounced
at the grain development stage (14 DAA) and continued up to
the senescent stage (28 DAA). On the other hand, ABA treat-
ment augmented proline accumulation in all the leaves of rice
and wheat cultivars (Table 19). The effects of BA and ABA
were greater in the flag leaf than in the second leaf at the
senescent stage of Rasi rice cultivar, but in Kalojira rice
and Sonalika wheat cultivars, an opposite trend was noted.

# D I S C U S S I O N

Although a great deal of experimental results has been
accumulated, the exact mechanism of monocarpic senescence,
particularly at the molecular level, still remains unsettled.
However, the evidence suggests that monocarpic senescence
is correlatively controlled and  there  is no  doubt that
reproductive parts exert regulatory influence in the mani-
festation of monocarpic senescence. Among monocarpic plants,
there are many different patterns in the relation of the
time course of leaf senescence (287). In the present inves-
tigation, the patterns of leaf senescence have been studied
in several rice and wheat cultivars in order to get  an
insight into the correlative control and the possible cause
of monocarpic senescence in rice and wheat plants. To analyse
the cause(s) of different patterns of senescence in these
cultivars and to explore the role of mobilization of meta-
bolites in the development of these senescence patterns,
some physiological, biochemical, anatomical and hormonal
studies were carried out in intact as well as surgically
altered cultivars of rice and wheat.

Degradation is an essential feature of the senescence
process and some quantitative measures are essential for
understanding the developmental events occurring during

the senescence process. Previous studies from this labora-
tory indicated that the loss of chlorophyll and protein
(32,35,257,339) and the loss of mineral nutrients, parti-
cularly nitrogen and phosphorus might serve as reliable
indicators of the progressive senescence during reproductive
development, at least in rice (256) and wheat (111) plants.
Hence, in the present investigation the loss of above para-
meters was taken as indicators of senescence and an index
of mobilization of metabolites from source to sink.

## 2.4.1. Studies in the leaf senescence behaviour of rice and wheat :

2.4.1.1. Two distinct modes of senescence patterns during
whole plant senescence of rice and wheat cultivars have
been reported (35,257). In the sequential mode of senescence
the leaves senesce in a chronological order which means that
leaf senescence is a function of leaf age. Whilst in the non-
sequential mode, such age-related senescence could not be
observed as in some rice cultivars, where the younger flag
leaf senesces earlier than the older second leaf (257,339).
The results of the present study with different rice and
wheat cultivars reveal that the flag leaf of short-statured
Rasi and Sashyasri rice cultivars demonstrated a nonsequential
mode of senescence. Thus, there was a dramatic change in
the decline of chlorophyll and protein in the flag leaf at
the grain maturation stage (21 DAA). In these two rice

cultivars the loss of chlorophyll and protein and the percentage of leaf yellowing were larger in the flag leaf than in the second leaf (Figures 1,2 & 4), And they became more prominent at the senescent stage (28 DAA). On the other hand, in medium-statured Kalojira and Badsabhog rice and Sonalika and Kalyansona wheat cultivars, a sequential mode of senescence was observed, where the loss of chlorophyll and protein and increase in percentage of leaf yellowing were proportional to the leaf age (Figures 1 to 6) and the higher metabolic activity in terms of maintenance of chlorophyll and protein was noted in the younger flag leaf than in the older second leaf. These observations further confirm the earlier findings from this laboratory (257, 258), But the present study also included two other rice cultivars which showed an intermediate mode of leaf senescence. Thus, in tall-statured Patnai and Kalma rice cultivars, the loss of chlorophyll and protein and the percentage of leaf yellowing were more or less equal in the flag and the second leaf at the senescent stage and the two leaves senesced almost simultaneously (Figures 1,2 & 4). Hence, these two rice cultivars could not be categorized under either sequential or nonsequential mode as reported earlier and they) showed an intermediate mode. The existence of these different patterns of leaf senescence in rice and wheat cultivars indicates that the senescence signal or death hormone may not be involved in inducing different patterns of leaf senescence in these cereal cultivars.

There is a distinct delimitation between reproductive parts
and vegetative parts in cereals, and thus, any signal or
death hormone originating in the panicle and moving down-
ward would have first induced senescence in the nearest flag
leaf in all the cultivars of rice and wheat reported here.
Had it been the case, all rice and wheat cultivars would have
shown a nonsequential mode of senescence, i.e., the flag leaf
would have invariably senesced first regardless of species
and cultivars due to its closest proximity to reproductive
parts, But this was not true. The fact that both sequential
and intermediate modes of leaf senescence also occur in rice
and wheat cultivars apparently suggests that the senescence
signal was not coming from the panicle, at least in rice and
wheat cultivars.

2.4.1.2. If it is assumed that nutrients are mobilized from
the nearer leaves to the developing seeds, there will be a
gradual decrease of the mineral status of leaves during the
progress of reproductive development. Also, a correlation
between declining mineral status and the leaf senescence
may be expected if deprivation of minerals and metabolites
is governing the manifestation of senescence syndrome. In
fact, the present study, where two most important mobile
nutrients, nitrogen and phosphorus, were taken as indicators
of mineral status of leaves (256), points in that direction.
Thus, in short-statured Rasi rice cultivar, which represents

a non-sequential mode of whole plant senescence, the loss
of these nutrients was more pronounced in the flag than in
the second leaf at the senescent stage (28 DAA) (Figures 8 & 9).
Interestingly, an opposite trend was observed in medium-
statured Kalojira rice and Sonalika wheat cultivars, which
are representatives of sequential mode of whole plant senes-
cence. In fact, in these cultivars the loss of nitrogen and
phosphorus in the three uppermost leaves below the panicle
was exactly proportional to their leaf age (Figures 8 & 9).
On the other hand, in the tall Patnai rice cultivar, which
represents an intermediate type, the loss of these nutrients
is more or less equal in the flag and the second leaf of
different maturity status. Although Derman  et al.(89) obser-
ved transfer of nitrogen from leaves to fruits in soybean
before visible leaf yellowing, they failed to correlate such
withdrawal of nutrients with the onset of senescence in
soybean. However, the present study clearly reveals that
loss of nutrients   such as nitrogen and phosphorus from
the leaves could be well correlated with the patterns of
whole plant senescence in different rice and wheat cultivars.
These results, thus, seem to suggest that loss of nutrients
from leaves exerts regulatory influence on the manifestation
of different modes of senescence observed in different rice
and wheat cultivars.

2.4.1.3. To elucidate further the possible relation between
mobilization of nutrients from leaves to grains and modes of
leaf senescence demonstrated by different rice and wheat cul-
tivars, the pattern of $[^{32}P]$-phosphate export from leaves
to grains and retention of the same by the fed leaves were
analysed. Apparently, the data favour the view that mobili-
zation of nutrients from leaves to grains is an important
factor in determining different modes of senescence manifes-
ted by different rice and wheat cultivars. The export of
$[^{32}P]$-phosphate per leaf basis was significantly greater
from the flag than from the second leaf in all the rice and
wheat cultivars, which reached a maximal point at the grain
development stage (14 DAA), declining thereafter (Figure 10).
This suggests that flag leaf is the main exporter of nutri-
ents to the grains, perhaps due to its greater proximity to
the sink (Figure 10). When measured per unit leaf area
basis (Figure 11), the export of $[^{32}P]$-phosphate was maximal
from the flag leaf of Rasi followed by that of Kalojira rice
and Sonalika wheat and Patnai rice cultivars. The leaf area
data depicted in Figure 4 further reveals that the export
of $[^{32}P]$-phosphate was inversely proportional to the area of
the flag leaf in different cultivars. The area of the flag
leaf of Rasi was minimal, but the export of phosphate isotope
was also maximal in this cultivar. However, this was just
opposite in other cultivars. Thus, the flag leaf of Rasi
undergoes greatest nutrient deprivational stress at the

grain development stage (14 DAA) and registered the earliest senescence syndrome. Conceivably, the difference in export between the flag and the second leaf was more pronounced in Rasi than in either Kalojira or Patnai and the difference was much less in the latter cultivars suggesting that both the flag and the second leaf equally participated in the process of nutrient export and the second leaf, being older than the flag leaf, senesced earlier. The pattern shown by Sonalika wheat cultivar exactly followed the same trend as that in Kalojira. Working with the Vigna radiata, Rao and Ghildiyal (335) have suggested that sink itself is instrumental in hastening the declining photosynthesis and the leaf senescence by effecting directly the mobilization and reutilization of nitrogen. The results of the present study also suggest that leaf became exhausted owing to increasing sink demand of the developing grains.

The data of retention capacity of $[^{32}P]$-phosphate of fed leaves (Figure 12) reveal that the isotope retention capacity remained greater in the second leaf than in the flag leaf of Rasi even at the senescent stage. This suggests that the metabolic activity remained greater in the second than in the flag leaf of this cultivar at the senescent stage. On the other hand, the capacity for retention of $[^{32}P]$-phosphate in Kalojira rice and Sonalika wheat was identical and always greater in the flag than in the second leaf which was in accordance with the maturity status of the

leaves (Figure 12). However, in Patnai, although the pattern of retention of phosphate isotope was similar to that of Kalojira rice and Sonalika wheat cultivars particularly at the earlier stages of reproductive development, the retention capacity of the isotope by both flag and second leaf of this cultivar became more or less equal at the senescent stage (Figure 12). If we consider $[^{32}P]$-phosphate retention capacity as an indicator of leaf metabolic activity, it will be evident that the retention capacity was proportional to the leaf maturity status in the cultivars Kalojira rice and Sonalika wheat, which were showing sequential mode of senescence. Interestingly, the situation was quite opposite in Rasi showing non-sequential mode of senescence. In the cultivar Patnai, where both the flag and the second leaf senesced almost simultaneously, also registered an equal $[^{32}P]$-phosphate retention capacity by the flag and the second leaf.

If we cast a glance at the $[^{32}P]$-phosphate mobilization data shown in Figure 10, it will be revealed that the export of $[^{32}P]$-phosphate from the leaves was greatest in Patnai followed by Kalojira and Rasi and least in Sonalika. That this export was directly proportional to the sink strength can be substantiated from the data of total weight of panicle in different cereal cultivars studied (Table 1). Thus, it is clear from the data that among the rice cultivars the export of $[^{32}P]$-phosphate was maximal in Patnai where the

sink strength (panicle weight) was also maximal. On the
contrary, the export of $[^{32}P]$-phosphate from leaves  to
grains was minimal in Rasi where the sink strength was also
minimal. These results thus suggest that sink demand  of
different rice and wheat cultivars exerts a regulatory
influence on the export of nutrients from leaves. Whether
active sinks, such as developing fruits, function only in
a passive manner by consuming soluble nutrients thereby
driving a mass flow system (73) or whether sinks send some
hormonal regulatory signals to the supply organs to regu-
late their activity (289, 290) cannot be said from these
results with certainty. Nevertheless, it is certain that
the rate of senescence has a relationship with mobilization
of nutrients which seems to be proportional to the sink
size in rice and wheat cultivars. MacKown et al.(218) have
recently reported that labelled N in wheat is translocated
to the reproductive parts according to the sink strength
and this is in full agreement with the $[^{32}P]$-phosphate
export data presented here.

2.4.1.4.  It is well known that supply of water, mineral
nutrients and cytokinins from roots to leaves influences
the rate of senescence (115,276,278,450). During monocarpic
senescence in soybean several authors have shown that root
growth ceases, degenerative changes occur and net mineral
accumulation declines (89,281,283). Roots generally provide

cytokinins and minerals required for maintenance of foliar function and pod development. It has been suggested that changes in the rate of delivery of xylem solutes have regulatory effect on leaf senescence and regulate soluble protein and chlorophyll level (234), as also photosynthetic gas exchange and stomatal resistance (143). In the present study the export of $[^{32}P]$-phosphate from the isotope-fed roots to the leaves was taken as an indicator of mobilization of nutrients from roots to leaves. The data presented here reveal that there was a gradual decline in the export of $[^{32}P]$-phosphate from roots to leaves in all rice and wheat cultivars (Figure 13). An analysis of the pattern of mobilization of this isotope in Rasi rice cultivar shows that $[^{32}P]$-phosphate was exported significantly at a greater extent to the second than in the flag leaf and least so in the third leaf. Thus, not only greater export of metabolites from the flag leaf to the grains, but also lesser entry of nutrients (and possibly root-originated cytokinins) into this leaf might possibly be the major reasons for earlier senescence of the flag leaf than the second leaf. In contrast, the export of $[^{32}P]$-phosphate from roots was larger in the flag than in the second leaf (Figure 13) in Kalojira rice and Sonalika wheat cultivars and it seems clear that the flag leaf of these cultivars received greater supply of nutrients (and also cytokinins) from the roots compared with the second leaf which enabled it to acquire greater sustenance

capacity and hence senescing later than the second leaf.
In Patnai rice cultivar, the export of $[^{32}P]$-phosphate
from roots to the flag and the second leaf did not differ
appreciably (Figure 13) and senesced almost simultaneously.
The above results, therefore, point out that the supply of
nutrients from roots to the leaves varies in different
cultivars and possibly plays a role in modifying the leaf
senescence behaviour. Such differential export patterns
from roots to leaves not only seems to depend on the meta-
bolic status of roots and leaves.but also on the vascular
architecture of the specific plant concerned. This will be
evident from the studies that follow.

2.4.1.5. To substantiate the above view, the number of
vascular bundles at the juncture of leaf lamina and leaf
sheath, the area of xylem vessels in a bundle and the lumen
of the largest vessel were recorded in three rice and one
wheat cultivars (Table 2). Kishitani and Tsunoda (187)
could obtain a positive correlation between total cross-
sectional area of xylem vessel at the leaf base and leaf
area with the photosynthetic rate and water supply. Thus,
in short-statured Rasi rice cultivar, showing non-sequential
mode of leaf senescence, the above xylem parameters were
greater in the second than in the flag leaf and the data
of the previous experiments also provided evidence of
greater nutrient supply to this leaf. It can, therefore,

be concluded that supply of nutrients (and also cytokinins) from roots to leaves can be regulated and restricted by the vascular architecture prevailing at the juncture of leaf lamina and leaf sheath, which plays an important part in regulating leaf senescence behaviour of the plant. This will be further clear if we analyse the xylem parameters of Kalojira and Patnai rice and Sonalika wheat cultivars (Table 2) where the data of $[^{32}P]$-phosphate export from roots to leaves and the mode of leaf senescence could also be well correlated. It can be documented in the literature that the fibrovascular tissue system of a plant regulates supply of water, mineral nutrients and cytokinins from roots to the leaves which can eventually modify leaf senescence and that the hydraulic architecture of the shoot also plays a major role in the regulation of leaf senescence (269,273, 277,281,291).

## 2.4.2.  Effect of phytohormones on whole plant senescence of rice and wheat :

2.4.2.1.  It is well known that phytohormones as foliar sprays can modify senescence of leaves attached to the plant depending upon the species and leaf maturity status (32,35, 87,281,297,351,339). Among the phytohormones, cytokinins almost universially retarded senescence of leaves. Next to cytokinins, $GA_3$ has been found to retard senescence in many cases (249,272). However, auxin is the least effective

hormone in this respect (167). Nooden (285) also reported
that a combination of (BA + $GA_3$) synergistically delayed
senescence of soybean plants. On the other hand, ABA and
ethylene promote senescence of the whole plant in a majo-
rity of the cases. In the present investigation, BA, $GA_3$
and their combination (BA + $GA_3$) and ABA were used as foliar
sprays to examine their effects on the modification of non-
sequential and sequential modes of senescence (two extreme
types) as observed in rice and wheat cultivars. The study
reveals that none of these hormones could change the pattern
(i.e., non-sequential and sequential) of senescence charac-
teristic of a particular cultivar. However, BA, $GA_3$ and
their combination retarded senescence of all the leaves over
their control, the combination treatment being most effec-
tive, whereas ABA accelerated senescence in these cultivars
(Table 3 to 6). The most interesting feature of this study
is that, although the hormones could modify the senescence
of leaves, they failed to modify the pattern of whole plant
senescence shown by a particular cultivar. It is to be noted
that the application of BA, $GA_3$ and their combination
(BA + $GA_3$) could reduce the difference in the contents of
chlorophyll and protein between flag and second leaf in
all the cultivars which became most pronounced at the sene-
scence stage in untreated control plants. ABA treatment,
on the other hand, markedly increased such difference in
the levels of above cellular components in the flag and

second leaf over the untreated control plants in these
cultivars (Table 5). It is noteworthy that effects of all
these phytohormones, regardless of their senescence retard-
ing or promoting effects, became evident only at the later
stages of reproductive development suggesting that the
sensitivity of attached cereal leaves to these phytohormones
was much less at the earlier stages of reproductive develop-
ment. It may be assumed that since the effects of these
phytohormones on the total longevity of these plants were
rather small, being only effective at the very late stage
of reproductive development, they failed to impose any modi-
fication on the mode of whole plant senescence observed in
these cultivars.

2.4.2.2. Since depletion of mineral nutrients from leaves
during reproductive development is an important characte-
ristic of monocarpic senescence (56,89,132,268,291,383),
it will be worthwhile to study the effects of above phyto-
hormones on the changes in nitrogen and phosphorus contents
of the leaves during the progress of reproductive develop-
ment in rice and wheat cultivars (Tables 7 to 10). The
study reveals that the application of senescence retarding
hormones, such as BA, $GA_3$ and their combination, also retar-
ded the loss of these nutrients from the leaves in accordance
with the senescence behaviour of leaves of each cultivar of
rice and wheat (Tables 7 to 10). Expectedly, the senescence

promoting hormone ABA rather accelerated the loss of these
nutrients, thereby creating greater depletion in the leaves
and consequently their earlier senescence. Even though the
application of these phytohormones could delay or accelerate
the loss of nitrogen and phosphorus from leaves of these
cultivars, they failed to alter the specific trend and
pattern of depletion of these nutrients shown by the leaves
of control plants of each cultivar. Thus, the depletion of
these nutrients could be correlated with the mode of sene-
scence displayed by a particular cultivar, notwithstanding
that such depletion was either delayed or accelerated by
phytohormone application.

2.4.2.3. In order to critically assess the role of senes-
cence retarding and promoting hormones on mineral redistri-
bution, the pattern of export of labelled phosphate from
leaves to grains and the retention capacity of the leaves
were studied in BA- and ABA-treated rice and wheat culti-
vars (Tables 11 & 12). The results reveal that BA signifi-
cantly increased export of $[^{32}P]$-phosphate as well as the
retention capacity of the fed leaves (Table 11), whereas
ABA caused an opposite effect in all the cultivars (Table 12).
It is interesting to note that although BA and ABA exerted
an influence on the export and retention capacity of $[^{32}P]$-
phosphate, the pattern remained essentially the same as
that of leaves of untreated control plants in all these

cultivars. This is reminiscent of the observations made by Mondal and Choudhuri (257) in some other rice cultivars. The higher export and retention capacity of $[^{32}P]$-phosphate by the leaves treated with BA may be attributed to higher synthetic and metabolic activity of BA-treated leaves (91, 198,304,423), while the lower export and retention capacity of radiophosphate in ABA-treated leaves may be interpreted as due to lower metabolic activity and higher degradative processes induced by ABA in treated leaves (104, 289,304, 370).

### 2.4.3. Role of certain biochemical and enzymatical changes in the senescence development in rice and wheat :

It is now well recognized that gene action is mediated by gene products which characterize the particular tissues and particular stages of development (43,203). Thus, the appearance and then disappearance of gene products are characteristic features of developmental cycles (92). However, senescence is regulated by a set of genes acting in concert and it is a carefully orchestrated phenomenon resulting in the controlled dismantling of specific cell structures (43, 291,410,455). Implicit is the idea that senescence results from programmed changes in gene products. Results of the present study provide evidence of changing patterns of RNA and histone protein in different leaves of rice and wheat cultivars. These two biomolecules seem to

play an important role in the execution of programmed sene-
scence (191,376,388). The present experiment shows that there
was a decrease in RNA and increase in histone protein and
decrease in the ratio between RNA and histone in the leaves
of all the rice and wheat cultivars according to their mode
of senescence (Figures 15 & 16). It may be emphasized that
there exists an inverse relationship between changes in RNA
and histone protein. And the decrease in the ratio of RNA/
histone seems to be a consistent indicator of ageing and
senescence rather than the changes in their individual com-
ponent. Furthermore, their changes were most easily discer-
nible prior to senescence of a particular leaf, implicating
their active involvement in the senescence process. It is
documented in the literature that chromosome-associated
histone protein increases and RNA decreases during ageing
and senescence of leaves (43,94,252,351,368,410,452,455)
which further corroborates the present findings. Application
of BA and ABA to the leaves on these cultivars appropriately
modified these changes (Table 13), pointing-out their regu-
latory effects on genes and gene products associated with
senescence development. It is now  well known that histone
protein inhibits the ability of DNA to serve as a template
for RNA synthesis (180,204,390). Petel and Berlyan (317)
have also shown a close relationship between DNA/histone
ratio and RNA content, and the decrease in H1 histone has
also been correlated with transcriptionaly poised chromosome

structure (69). From the observations of decline in RNA
and RNA/histone ratio and slow rise in histone protein in
the leaves approaching senescence in different rice  and
wheat cultivars, it can be assumed that the major synthetic
activities are perhaps gradually switched off and the degra-
dative processes switched on during ageing and senescence.

Another spectacular manifestation of switching on of
the degradative processes during ageing and senescence is
the protein breakdown resulting from high protease activity
and the consequent rise in free amino acids in leaf tissues.
The liberated free amino acids along with other nitrogenous
substances produced during senescence are eventually trans-
located to the developing grains to meet their demand  for
nitrogen assimilation (323). The present study also confirms
this. The loss of protein in leaves of different rice and
wheat cultivars could be correlated with the rise in protease
activity with the concomitant accumulation of free amino
acids. This was also found to be a function of senescence
pattern of leaves. Thus, in the cultivar Rasi, which shows
non-sequential mode of leaf senescence, the changes in pro-
tease activity and accumulation of free amino acids in leaves
were also found to be non-sequential (Figures 17 & 18).
Whereas, in the sequential mode of senescence, manifested by
Kalojira rice and Sonalika wheat cultivars (Tables 17 & 18),
their changes were also sequential, i.e., proportional to
the leaf age. The greatest accumulation of free amino acids

in leaves due to proteolysis could be observed at the grain
maturation stage, but there was a decline afterwards sugges-
ting that both demands for nitrogen by the sink (panicle)
and the supply by the source (leaves) are perhaps reduced
prior to senescence. The maintenance of high protease acti-
vity until complete senescence of leaves might suggest that
protein breakdown occurred till very late stage of senescence.
However, lesser accumulation of free amino acids in leaves
during this period may apparently appear to be conflicting,
But this apparent contradiction may be interpreted as due
to known involvement of free amino acids in the synthesis
of different hydrolytic enzymes associated with senescence
(396) and also in meeting the nitrogen demand of other vege-
tative parts which are yet to senesce (351).

The deferment of senescence by the application of BA
and its promotion by ABA are also reflected in protease
activity and free amino acid accumulation (Table 14), impli-
cating a regulatory role of these phytohormones in protein
turnover (289,423). Regardless of the particular pattern of
senescence displayed and the initiating and controlling
factors involved, the senescence of individual leaf of the
cereal cultivars seems likely to be similar at the cellular
level. And the present study is indicative of the fact that
a balance between senescence retarding and promoting hormones
at the cellular level may be one of the important controlling
factors of senescence development.

Cellular membranes are selective, dynamic barrier that play an essential role in regulating biochemical and physiological events and the deterioration of membrane is an early fundamental feature of the senescence process (411). Thus, during senescence there is progressive loss in membrane integrity resulting in a rise in membrane permeability. Most of the proteolytic enzymes are known to be located in the vacuoles, while majority of the proteins are located in the chloroplasts (112,220,221,402,438). It follows, therefore, that membrane damage is necessary for protein breakdown and senescence development. It has been postulated by Veierskov and Thimann (424) that senescence process is facilitated by gradual impairment of vacuolar membrane, allowing proteases to enter into the cytosol and attack the proteins there and in the organelles. Free radical-mediated lipid peroxidation is an important mechanism causing membrane deterioration during senescence (411). The accumulation of free radicals during ageing and senescence is also known to augment lipid peroxidation and one of the reasons for their accumulation is the gradual loss of activities of free radical scavenging enzymes such as superoxide dismutase (SOD), catalase and peroxidase. The present study with different cultivars of rice and wheat also supports the above hypothesis. Thus, there was senescence-related proportional increase in the level of malondialdehyde (MDA), which is the oxidation product of polyunsaturated membrane fatty acids and a reliable

indicator of membrane deterioration, in leaves of different
rice and wheat cultivars (Figure 19) pointing out that mem-
brane deterioration is the function of ageing and senescence
in these cultivars. That such membrane deterioration is
induced by free radicals can be indirectly substantiated
from the observations of the decline in the activity of SOD
and catalase in leaves with the approach of senescence
(Figures 19 & 20) favouring accumulation of oxy free radicals
which might lead to membrane deterioration. It has been
amply demonstrated by a number of workers that $H_2O_2$ is the
stable product of oxy free radicals generated in tissues (96)
and the involvement of $H_2O_2$ in the senescence of leaves has
been demonstrated in various plants (61). The rise in pero-
xidase activity during senescence along with $H_2O_2$ may also
facilitate oxidative degradation of cellular macromolecules
and such a rise in peroxidase activity was also noted in
leaves of rice and wheat cultivars (Figure 20). The accumu-
lation of MDA and changes in free radical scavenging enzymes
were most pronounced at the senescent stage of rice and wheat
cultivars. All these results seem, thus, to indicate that
progressive loss of free radical scavenging enzymes, which
favour accumulation of free radicals and $H_2O_2$, may lead to
membrane deterioration in leaf tissues and consequently
senescence.

The external application of BA significantly retarded
MDA accumulation and enhanced the activities of free radical
scavenging enzymes (Tables 15 & 16) as mentioned above, while
ABA caused an opposite effect. Thus it may be assumed that
one of the mechanisms of phytohormones retarding or promoting
senescence of plant tissue is mediated by regulating free
radical scavenging enzymes such as SOD, catalase and peroxi-
dase and modulating free radical-induced lipid peroxidation
and membrane damage.

## 2.4.4. Role of transpiration in the regulation of senescence:

Transpiration seems to play an important role in the
regulation of monocarpic senescence because the supply of
cytokinins, nutrients and water to the aerial parts is partly
dependent on the transpiration pull along the stem axis (115,
157,174,281,289,384). The present study shows that rate of
transpiration by the whole plant (main tiller) gradually
decreased in rice and wheat cultivars during their reproduc-
tive development (Table 17). The rate of transpiration also
decreased in accordance with the mode of senescence in these
cultivars. Such decrease in the rate of transpiration may be
related with age of leaves, since stomata are known to fully
or partially close in aged tissue of many plants (403,405).
While treatment of plants with BA significantly increased
the rate of transpiration by the whole plant as well as by

individual leaf, ABA spraying strongly inhibited the same in all the cultivars studied (Table 18). It is documented in the literature that cytokinins keep stomata open, while ABA causes stomata to close (160,171,231,333,403). The effects of BA and ABA in the present experiments can be interpreted on the basis of their regulatory influence on stomatal opening and closing. There are also reports that a decrease in cytokinins and an increase in ABA level take place during ageing and senescence in plants (85,118,300, 360,436). The occurrence of such a situation under natural condition may strongly favour stomatal closure that presumably be responsible for the reduction of transpiration in different rice and wheat cultivars during progressive ageing.

The accumulation of proline in stressed tissues is a widely reported observation (46,324,393,395). Proline accumulation during ageing and senescence has also been reported in isolated (394,430) as well as in intact leaves (260,392) of many species. Furthermore, it has been postulated by Biswas and Choudhuri (32) that mobilization of metabolites from leaves to grains in rice during reproductive development causes a deprivational stress in leaves. It was subsequently demonstrated by Ray and Choudhuri (339) that there was an increase in ABA-like substances due to such deprivational stress in rice leaves. That stress-induced ABA can, in turn, enhance proline accumulation in leaves is also well documented

(12,324,394). Like ABA, proline can also promote stomatal closure (333,334). Thus, the accumulation of both ABA and proline with ageing may serve as reliable indicators of whole plant senescence. In the present study it was observed that proline accumulation gradually increased in the leaves of all rice and wheat cultivars up to the grain maturation stage, but decreased thereafter (Figure 21). Thus, at the grain maturation stage maximal accumulation of proline took place in the flag leaf of Rasi, while it was in the second leaf in Kalojira rice and Sonalika wheat cultivars. These results fit in well with the observed modes of senescence in these cultivars. The maximal accumulation of proline at the grain maturation stage suggests that the leaves had undergone maximal stress prior to this stage. The data of $[^{32}P]$-phosphate export, discussed earlier (Figure 10), show that maximal mobilization of metabolites took place at the grain development stage. Thus, it may be assumed that the leaves were subjected to maximal deprivational stress at the grain development stage (14 DAA) and such an assumption finds support from the observation of proline accumulation at the grain maturation stage (21 DAA). Our data, therefore, lend further credence to the postulation made by Biswas and Choudhuri (32) as alluded before. A large number of reports shows that the application of ABA induces proline accumulation in the treated tissue (12,324,392,394). However, the effect of cytokinin on proline accumulation has been scarcely reported (260,395). Nevertheless, the retardation of proline

accumulation by BA and its acceleration by ABA treatment
in leaves of rice and wheat cultivars (Table 19) suggest
that proline accumulation is one of the characteristic
features of senescence syndrome and may be intimately
involved in the process of senescence development. From
the evidence presented here it may be assumed that retarda-
tion of the accumulation of proline by BA and its promotion
by ABA treatment may presumably be mediated by decreasing
or increasing the internal nutrient deprivational stress,
respectively.

## 2.4.5. Hormonal mechanism of regulation of senescence :

In recent years, several studies have emphasized the
regulatory role of endogenous cytokinins and ABA in the
senescence process of the whole plant or detached organs,
particularly leaves (9,32,64,278,283,297,300,351,384,403,
423). It is also well known that ethylene plays an impor-
tant role in leaf abscission but its role in leaf senescence
is not very clear. Several workers, however, have suggested
that ethylene acts as a senescence promoting hormone (1,5,
119,176). It has also been demonstrated that during senes-
cence the release of endogenous ethylene increases ( 5,176).
Reports concerning the decrease in endogenous cytokinin-like
(CK-like)substances and the rise in endogenous ABA level
during ageing and senescence of leaf tissues are also not
very uncommon in the literature (32,60,84,118,174, 211,291,
300,302,303,339,436). The present study with different rice

and wheat cultivars also supports the above findings. The study shows that CK-like substances gradually decreased in all the leaves of both rice and wheat cultivars during the progress of reproductive development (Figure 22). In Rasi, the decline in CK-like substances was much greater in the flag than in the second leaf. In contrast, an opposite trend was observed in Kalojira rice and Sonalika wheat cultivars. These findings are in complete agreement with the observed mode of senescence in these cultivars. In general, the decline in CK-like substances may presumably be ascribed to the decline in root cytokinin production (85, 184,294,300) which may also be correlated with lowering of transpiration pull (21,115,150). The little cytokinins that are still produced by the roots may be translocated to the developing seeds instead of leaves because of greater sink demand of the former (211,287,289,357,436). Such a view gets its support from the observation that depodding increases CK-level in leaves and delays senescence in soybean (300). The decline in cytokinin in leaves may be also responsible for inhibiting the synthetic processes and promoting the degradative processes (32,35,173,174,259, 289,460).

Concomitant with the decline in CK-like substances in leaves, the level of ABA gradually increased up to the grain maturation stage, declining thereafter in rice and wheat cultivars (Figure 23). The decline in ABA in the flag leaf

of Rasi was faster than that in the second leaf. Whereas in Kalojira rice and Sonalika wheat cultivars, the level of ABA increased in chronological order of the leaves (Figure 24). Thus, earlier accumulation of ABA in the flag leaf of Rasi and in the second leaf of Kalojira rice and Sonalika wheat cultivars with the simultaneous decline in CK-like substances prior to senescence development appears to be an important factor regulating monocarpic senescence of cereal plants. The external application of these two hormones also exerted their regulatory effects on the whole plant senescence of these cultivars. The effect of ABA on the whole plant senescence may presumably be mediated through retardation of many physiological and bio-chemical processes such as photosynthesis, protein synthesis stomatal closure etc (118,134,289,291,345,351,370,403).

It is noteworthy that the ratio of CK-like substances and ABA gradually decreased with the progress of reproduc-tive development in both rice and wheat cultivars. The maximal decrease was observed at the grain maturation stage (21 DAA), which just preceded the senescent stage (28 DAA). All these results seem, thus, to suggest that a critical balance between these two hormones has a profound regula-tory influence on the development of monocarpic senescence in cereal plants. This is in complete agreement with the view of several workers (95,101,351). But it is not yet

clear from these results what actually triggers the initia-
tion of monocarpic senescence in these plants.

Among the known hormones, the role of ethylene in whole
plant senescence is most conflicting, although ethylene has
been suggested by many workers to act as a senescence pro-
moting hormone in attached and detached leaves of many
species (1,5,176,241,332,458). Aharoni et al. (7)
have reported that ethylene production decreased in the
first phase of senescence and there was a transitory rise
in ethylene production during the phase of rapid chlorophyll
loss. From our data it could be stated that the release of
ethylene was the function of leaf ageing and senescence
development in different rice and wheat cultivars (Figure 25).
Thus, with the approach of senescence, the release of ethy-
lene also increased. The rise in ethylene production was
significantly faster at the later stage of reproductive
development in both rice and wheat cultivars. The difference
in ethylene production between the flag and the second leaf
of Kalojira (rice) and Sonalika (wheat) was not as prominent
as that of Rasi. That ethylene plays a regulatory role in
petal senescence has recently been demonstrated by Lawton
et al (203) in carnation. It has also been reported by
Woodson (448) that flower senescence in carnation is asso-
ciated with changes in gene expression involving both pro-
tein and in RNA changes. The early rise in ethylene in
leaves during anthesis stage suggests that ethylene might

also play a similar role in cereal leaf senescence as
has been observed in carnation petals. One interesting
finding reported by Schwabe and Kulkarni (366) is that
severé water stress, which was accompanied by a signifi-
cant rise in ABA in detached leaves of <u>Kleinia articulata</u>,
did not lead to senescence unless combined with ethylene
treatment and postulated that while ABA might play an
important role in leaf senescence, its lethal effect could
not be realised until and unless ethylene-induced membrane
changes would also synergistically assist. External appli-
cation of ethylene has also been reported to enhance various
senescence-related processes in plants (176,313,447). From
all these observations along with those reported here, it
may be concluded that a decline in CK level and a rise in
ABA and ethylene levels in plants during their reproductive
development are intricately involved in the senescence
development of different cereal cultivars.

### 2.4.6. <u>Changes in nucleic acids and proteins in the shoot apex during transition from vegetative to flowering stage of rice and wheat cultivars</u> :

It has been observed that the transition from the vege-
tative to the reproductive stage is accompanied by profound
physiological, biochemical, genetical and hormonal changes
in plants (25,78,126,131,164,165,195,217,371). Since deve-
lopmental processes are genetically programmed, the gene
products are also accordingly changed for the execution of

this programme. Evidently, characteristic changes are expected
to occur in nucleic acids and proteins, the main biochemical
agents for the execution of the developmental programme dur-
ing transition from the vegetative to the reproductive stage.
In the present study we, therefore, attempted to analyse
changes in some important biomolecules deemed to be associa-
ted with such transition. Thus, changes in total protein,
DNA, RNA and histone protein were studied prior to this tran-
sition in two rice and one wheat cultivars. There was a sig-
nificant rise in protein, DNA and RNA in the shoot apex of
Rasi rice cultivar up to the plant age of 74-80 days, i.e.,
at least 12 days before panicle emergence and   there was a
decline thereafter (Figure 26). Interestingly, the histone
protein increased at the plant age of 77 to 80 days when
other biomolecules started declining. The same trend was also
noted in Kalojira rice and Sonalika wheat, varying only in
the time period (Figures 27 & 28). Histone protein is known
to act as an inhibitor of gene expression (180,388,390). The
critical rise in nucleic acids and total proteins and decline
in histone protein prior to transition from one phase to the
other suggests that profound gene activity may possibly be
required for panicle initiation in these cereal cultivars.
The decline in nucleic acids and protein and the rise in
histone protein perhaps mark the end of the transition pheno-
menon. From all these results it can be concluded that marked
changes in genetic materials as manifested by the changes in

the contents of nucleic acids and acidic and basic proteins
occur in the shoot apex prior to transition from the vegeta-
tive to the reproductive stage of these cultivars.

## 2.4.7. Surgical experiments :

2.4.7.1. Reproductive parts of monocarpic plants have been
reported to be the most important agents which influence the
whole plant senescence presumably by drawing metabolites
from the vegetative parts (nutrient drain hypothesis) and/or
supplying some as yet unknown senescence-inducing factor(s)
to the vegetative parts (senescence signal hypothesis). Thus,
it has been reported by the majority of the researchers that
removal of reproductive parts delays  senescence of the whole
plant (35,210,257,290,318,339,421), notwithstanding a few
reports to the contrary (8,65,137). The present experiments
showed that removal of panicle from Rasi and Kalojira rice
cultivars, either at the anthesis (O DAA) or at the grain-
filling stage (7 DAA), reduced the loss of chlorophyll and
protein over the intact control plants and delayed senescence
(Tables 20 & 21). The most interesting feature of panicle
removal experiment is that such treatment altered the mode
of senescence in Rasi, where the non-sequential mode was
changed to the sequential mode, as observed in Kalojira rice
and Sonalika wheat cultivars. Although removal of panicle
delayed the onset of leaf senescence in Kalojira rice and
Sonalika wheat cultivars, there was no change in the mode

of senescence (Tables 21 & 22). It may be noted that the
delaying effect due to panicle removal was more pronounced
if done at the earlier stages in all the rice and wheat
cultivars. This was also true for Rasi. This is imperative
because if the sink (panicle) is removed at earlier stages,
less nutrients will be drawn out from the source (leaves)
and evidently there will be delay in leaf senescence. And
this perhaps happened in the present case. Furthermore, if
any senescence factor from reproductive parts be involved
in initiating senescence, the possibility of its accumula-
tion in leaves would be less if the reproductive sink (panicle)
was removed earlier. Another interesting feature of this ex-
periment is that the delaying effect due to panicle removal
was more marked in rice compared with that in wheat. One of
the possible reasons of such difference may be ascribed to
the greater availability of current photosynthate produced
by the glumes and awns in wheat than in rice (40,100,185,
356,415), which possibly made it less dependent on source
leaf unlike that happened in rice. The evidence in favour
of this explanation may be provided from the data presented
here, which showed that the initial content of both chloro-
phyll and protein in glumes was significantly higher in
wheat than in rice, but the decline of these components was
much greater in wheat than in rice during reproductive deve-
lopment (Figure 29). This suggests that the contribution to
grain-filling from the flag leaf of rice was greater than

that of wheat (265) and conversely, the contribution of
ear parts to grain-filling was greater in wheat than that
in rice (414). It has been suggested by Biswas and Mondal
(35) that in wheat the glumes act as intermediateries in
the transfer of assimilates from leaves to grains and the
contribution of flag leaf is rather indirect. However, the
situation appears to be opposite in rice (259). This sugg-
estion could well be applied to the above observations made
by us in both rice and wheat.

The analysis of nitrogen and phosphorus contents of the
leaves of rice and wheat cultivars from which the panicle
was removed at the anthesis (O DAA) and grain formation
(7 DAA) stage showed that their contents decreased relatively
slowly in comparison to that of intact control plants with
the progress of reproductive development. Interestingly, the
removal of panicle after grain-filling stage (14 DAA) neither
reduced the loss of nitrogen and phosphorus nor delayed
senescence of leaves (Tables 23 to 25), suggesting that the
maximal sink demand possibly was developed around the grain-
filling stage (14 DAA) causing the greatest depletion of
nutrients in leaves and promoting senescence. The delayed
removal of panicle produced no eff~ct on the mineral con-
tents of leaves over the intact control plants suggesting
that the demand of nutrients from the leaves by the develop-
ing grains had already been met by the time the panicle was

removed. The removal of sink has been shown to increase the mineral level in leaves in many species (89,294,443,444). That the rate of senescence could be altered by sink size has also been demonstrated by several workers (72,73,74,75). However, it is also suggested by several workers that drawing of a large amount of metabolites from the vegetative parts by the developing fruits may be an important factor for rapid senescence in many monocarpic plants (32,35,253, 258,339). A similar conclusion has been also drawn by Davies and his coworkers working with G2 line of pea (139,182).

The fact that the decline in minerals from leaves, particularly nitrogen and phosphorus, is due to their export to grains could be demonstrated by isotope studies. In fact, $[^{32}P]$-phosphate isotope experiments revealed that the removal of panicle at the anthesis (0 DAA) or grain-filling stage (7 DAA) significantly increased the retention capacity of $[^{32}P]$-phosphate of all the three leaves and stem of rice and wheat cultivars (Tables 26 to 28). However, such an act of removal at the later stages of reproductive development (14 and 21 DAA) failed to increase the retention capacity of $[^{32}P]$-phosphate in the leaves. This suggests that export of major nutrients from the leaves to the grains became relatively insignificant after the grain-filling stage, since the maximal export of $[^{32}P]$-phosphate took place within 14 DAA after anthesis of rice and wheat cultivars. The isotopic

studies further substantiated the observation that the
developing seeds are less dependent on the leaves for the
metabolite supply in wheat compared with that in rice. The
rise in retention capacity of $[^{32}P]$-phosphate in leaves and
stem of plants from which the panicle was removed at the
earlier stages of reproductive development is likely to
be due to the absence of sink demand which remained maximal
at the earlier stages of reproductive development in intact
plants of rice and wheat cultivars.

2.4.7.2. Surgical alterations of the source-sink ratio may
provide some interesting clues to the specific involvement
of an individual leaf and the reproductive parts in the
whole plant senescence of rice and wheat cultivars. Thus,
in order to assess this, the plants were first subjected
to surgical alteration by defoliation treatment. The sene-
scence behaviour of the remaining leaves was studied after
excision of a particular leaf. The results clearly revealed
that the removal of the flag leaf had the most significant
effect on the enhancement of senescence of the second leaf
in all rice and wheat cultivars (Tables 29 to 31). Whereas,
removal of the second leaf, although enhanced the senescence
of the flag leaf, had less pronounced effect compared with
that observed in the second leaf when the flag leaf was
removed. The detachment of the third leaf, on the other
hand, produced little effect on the senescence of either

the flag or the second leaf. All these results seem to suggest that the flag leaf plays an important role in the mobilization of metabolites to the sink in these cereal cultivars. It is also to be noted that the effect of leaf removal on the senescence of remaining leaves was more pro- nounced in rice than in wheat. This again suggests that the involvement of leaves in the export of metabolites was less significant in wheat than in rice. These observations are in full agreement with those of Mondal and Choudhuri (258) in rice and Biswas and Mondal in wheat (39). Analysis of leaf nitrogen and phosphorus contents of the remaining leaves as well as $[^{32}P]$-phosphate retention capacity and export data of the plants from which a particular leaf was excised, lends further credence to the above suggestion (Tables 32 to 37). These data further point out that mobilization of nutri- ents and metabolites from the leaves to the panicle plays an important role in the senescence development of cereal plants. It was also clear from the results presented above that when the ratio of source to sink was lowered by exci- sion of leaves, particularly the flag or the second, the remaining leaves appeared to compensate the sink demand (312) which remained constant throughout and such a situation presumably enhanced the development of senescence in the remaining leaves due to augmented depletion of metabolites and the resultant exhaustion.

2.4.7.3. As previously stated, the reproductive structures
of monocarpic plants may act as a strong sink for drawing
nutrients and metabolites from leaves or may send some
senescence-inducing stimulus to the leaves or both. In
order to further clarify the role of reproductive structures
in inducing senescence of rice and wheat cultivars, we attem-
pted to examine the effect of removal of different percentage
of spikelets from the panicle or emasculation treatment on
the whole plant senescence of rice and wheat cultivars. One
of the most interesting features of rice cultivars is that
complete removal (100%) of spikelets induced the development
of a secondary branch at the axil of the second leaf unlike
that in wheat cultivar where no such branch development took
place  (Table 38 & 39). Furthermore, when the spikelets of
the secondary branch of rice was completely removed there
was development of the tertiary branch. However, no further
branch development occurred when the spikelets of the ter-
tiary branch itself were completely removed. The secondary
and tertiary branches contained only two leaves. Removal
of different percentage of spikelets from the panicle of the
main tiller or emasculation of the panicle in rice and wheat
cultivars produced some interesting results. Thus, the removal
of 50, 75 and 100 percent spikelets from the panicle  or
emasculation of the panicle in Rasi and Kalojira rice cul-
tivars caused an induction of secondary branch development
while the removal of 25 percent spikelet had no effect  on

branch development. Again, the removal of 75 and 100 percent
spikelets from the panicle or emasculation of the panicle
of the secondary branch was only effective in producing ter-
tiary branch, while the removal of 25 and 50 percent spi-
kelets from the panicle of the secondary branch produced no
branch, i.e., this did not induce the tertiary branch deve-
lopment (Tables 38 & 39). Interestingly, even complete removal
of spikelets from the tertiary branch or its emasculation
treatment failed to produce further branch development (i.e.
quaternary branch).

All these results seem, thus, to suggest that the sink
size in rice cultivars exerts a regulatory role on  the
secondary and tertiary branch development. However,  the
failure of quaternary branch development even after  the
complete removal of the panicle in the tertiary branch points
out that the sink size is not the only limiting factor in
inducing branch production. It can be observed from the
data of leaf area and seed production capacity of the main-
tiller, secondary and tertiary branches that there was a
gradual reduction in the number of seeds per panicle and
the area of the flag and the second leaf from the main tiller
to the tertiary branch (Tables 38 & 39). This leads to the
suggestion that a critical balance between the size of the
sink and the source was necessary for the induction of
branch development in rice cultivars. It appears that such

a balance was lost in the tertiary branch and hence no further branch development occurred at the leaf axil of this branch. These interesting results however need further critical evaluation.

It is clear from the above results that the reproductive parts (panicle) exerted an inhibitory influence on side branch development in rice plants comparable with the phenomenon of 'apical dominance'. Nevertheless, the complete inhibition of development of quaternary branch from the tertiary branch clearly indicates that some factor(s), associated with branch development, became limiting in the tertiary branch. As a consequence of this, there was no quaternary branch development and the above-ground parts of the plant completely senesced and died along with the tertiary branch. It is tempting to speculate that the apical dominance-like effect, as exerted by the panicle, appears to regulate the onset of whole plant senescence. Thus, the removal of a higher percentage of spikelets was necessary for destroying the apical dominance-like effect and inducing the development of tertiary branch than what was necessary for the induction of secondary branch development in both the rice cultivars studied.

Another factor which seems to be involved in this phenomenon is the leaf area. The seed production capacity of different branches was found to be directly related with the leaf area, since leaf is the main source for supplying photosynthate and other metabolites for the seed development (44, 232). It seems, therefore, that the initiation of side branches in rice cultivars was the consequence of a balance

between the inhibitory influence of the panicle and the
promotive influence of the leaf subtending the branch,
possibly mediated by metabolites and phytohormones. Evi-
dently, the failure of quaternary branch development at
the second leaf axil of the tertiary branch even after
complete removal of spikelets or emasculation treatment
seems to point out that the branch initiation factor(s),
possibly supplied by the second leaf of tertiary branch,
became limiting due to the reduction of leaf area below a
critical level. That the leaf provides an essential factor(s)
for the side branch development can be further corroborated
from the findings that complete removal of both spikelets
and the second leaf from the main tiller and similar treat-
ment of the secondary branch in both rice cultivars comple-
tely failed to induce secondary and tertiary branch develop-
ment, respectively. It is to be noted here that the removal
of spikelets from the main tiller of the wheat cultivar did
not initiate secondary branch development, suggesting that
inhibitory influence of the panicle is species specific.
However, there may be another possible reason for such diff-
erence observed in rice and wheat cultivars. In rice, the
grain-filling is largely dependent on the supply of photo-
synthate and metabolites from leaves, whereas in wheat the
reproductive parts also actively participate in the grain-
filling process, where the leaves often play a secondary
role. Thus, the removal of total sink in wheat cultivar

possibly did not cause sufficient alteration in the
cellular metabolites in the second leaf which seems nece-
ssary for branch development. A recent report by Bangerth
(14) shows that polar transport of IAA from the earlier
developing seeds inhibits the development of other seeds
and also observed a Primigenic dominance (PP), a kind of
correlative inhibition, in which the earlier developing
seeds inhibits later developing organs. Such transport of
IAA from the fruits has also been found to be closely related
to the number of seeds present (385) which inhibits lateral
bud formation. It has also been suggested by several authors
that cytokinins originating from roots possibly inhibit IAA
metabolism and promote lateral bud growth (154,325). The
application of cytokinin or IAA and a combination of both
in lanoline paste on the cut surface of the depanicled plants
had no influence on secondary branch development as noted in
the present study (data not shown). This suggests that the
apical dominance like influence of the panicle may be exerted
through some substance(s) other than IAA and/or cytokinins.
Admittedly, this can not be said with certainty unless
labelled IAA or cytokinins are used in such experiments.

Looking at the senescence behaviour of leaves of two
rice and one wheat cultivars after removal of different per-
centage of spikelets from the panicle or emasculation
treatment, one can easily infer that senescence was delayed

in both rice and wheat cultivars due to removal of spike-
lets or emasculation treatment and the delaying effect
gradually increased with increasing removal of spikelets
(Tables 40 to 42). Thus, the reduction of sink demand was
related to the progress of senescence, although complete
removal of the panicle (sink demand) did not prevent sene-
scence completely. This observation finds support from the
observations of Biswas and Mondal (39) in wheat, Valio and
Polo (421) in bean, Crafts-Brandner and Egli (73) in soy-
bean and Kelly and Davies (182) in G2 pea. Another interes-
ting feature of the present study is that a minimum of 50
percent spikelet removal from the main tiller was necessary
to induce secondary branch development at the second leaf
axil of the main tiller of Rasi cultivar as well as for
inducing a change from the non-sequential to the sequential
mode of senescence. To achieve such results in the secondary
branch of Rasi, a minimum of 75 percent spikelet removal
was necessary. Although there was a delaying of senescence
of leaves in Kalojira due to spikelet removal or emascula-
tion treatment, the sequential pattern of senescence  is
maintained throughout the reproductive development.

If one follows the pattern of leaf senescence of secon-
dary and tertiary branches, it will be seen that they always
showed sequential and non-sequential mode according to the
mode shown by the main tiller unless, of course the

spikelets were removed, suggesting that a particular mode
of senescence is genetically controlled. Although the
removal of 75 and 100 percent spikelets or emasculation
of tertiary branch delayed leaf senescence, quaternary
branch was not formed in either rice cultivar and conse-
quently the mode of leaf senescence behaviour in Rasi was
not changed in this branch, i.e.,it remained non-sequential
like the main tiller (Table 45) because there was no alter-
native sink at the second leaf axil of the tertiary branch.

It is noteworthy that the total longevity of the main
tiller (i.e. the whole plant) was extended by about 42 days
over the unexcised control plants owing to side branch
production at the second leaf axil. Hence it may be conclu-
ded that both leaves and reproductive parts might exert
regulatory role in side branch production, which, in turn,
might control the longevity of the whole plant. The sene-
scence inducing substance, if formed in the subtending
second leaf, was not transmitted to the leaves of the side
branch. Had this happened, the second leaf of Rasi would
have then senesced earlier than the flag leaf of the side
branch which was, however, not the case. Thus, in rice,
the failure of further branch production on removal  of
spikelets marks the end of the whole plant.

# CONCLUSION

It was observed in the present investigation that
among the rice cultivars studied, Rasi and Sashyasri showed
a non-sequential mode of leaf senescence, whilst Kalojira
and Badsabhog showed a sequential mode of leaf senescence.
The other two rice cultivars, Patnai and Kalma, showed an
intermediate type. Both the wheat cultivars (Sonalika and
Kalyansona), however, showed a sequential mode of senescence.
Conceivably, had the senescence factor come from the repro-
ductive parts (seeds), the flag leaf would have always
senesced first, regardless of cultivars due to its closest
proximity to the reproductive parts. But this was not the
case, since some rice cultivars showed non-sequential mode
of senescence. Recent observations of Davies and his co-
workers in G2 pea on the quantitative export from the fruit
to the apex and the identification of exported materials
as sucrose and malic acid, which are ineffective as sene-
scence inducing substances, led them to abandon the concept
of senescence signal hypothesis (139,182).

There was a distinct correlation between leaf senes-
cence behaviour with xylem parameters at the juncture  of

leaf lamina and leaf sheath in different rice and wheat
cultivars, suggesting that conducting vessels and  the
orthostichous connections between leaves and reproductive
parts play an important role in nutrient withdrawal process
from leaves to the reproductive parts, and also hormones,
mineral nutrients and water from roots to the shoot, thereby
determining senescence behaviour of the leaf.  In  wheat,
the pattern of leaf senescence appears to be less dependent
on metabolite supply from leaves, unlike rice, since the
reproductive parts of wheat themselves provide an appreci-
able amount of assimilates to the growing seeds which are,
therefore, less dependent  on the  source leaf for  their
nourishment. The period of maximal export of nutrients in
rice and wheat was generally found to be prior to  grain
maturation stage when maximal nutrient stress in the leaves
presumably developed as indicated by the largest proline
accumulation. Such a situation resulted in a great hormonal
disbalance favouring senescence development, i.e. depletion
of senescence retarding hormones, such as cytokinins (and
possibly $GA_3$), and accumulation of senescence promoting
hormones, such as ABA and ethylene.

Surgical removal of panicle (sink) or emasculation
treatment of the panicle at the early stages of reproductive
development, although delayed senescence by several  days,
could not prevent it in both rice and wheat cultivars and

all these cultivars showed a uniform pattern of sequential
leaf senescence possibly due to development of an alterna-
tive sink in the form of a secondary or a tertiary branch.
Similarly, external application of senescence retarding or
promoting hormones delayed or enhanced the senescence process
for a few days without altering the leaf senescence behaviour,
but failed to prevent senescence indefinitely in both rice
and wheat cultivars. In desinked rice cultivars, a secondary
branch developed at the second leaf-axil which also produced
a tertiary branch, if further desinked at the earlier stages
of reproductive development. Interestingly, the mode of leaf
senescence of 'daughter' branch was exactly the same as that
of the 'mother' plant from which it developed, suggesting
that the pattern of leaf-senescence exhibited by each cultivar
is an inherent and genetically controlled character of a
species or cultivar. Apparently, the above results seem to
suggest that nutrient withdrawal might not be the sole factor
in inducing the whole plant senescence, but, no doubt, this
was a major senescence accelerating factor in these cereal
cultivars. While in rice, it could be interpreted as due to
the development of a secondary branch at the leaf axil as
an alternative sink and hence the nutrient export from the
'mother' plant to the 'daughter' branch remained unabated,
it could not, however, be explained in wheat cultivars where
there was no development of an alternative sink in the form
of a secondary branch. One of the reasons of the failure of

secondary branch development in wheat plants might be
speculated as due to their leaf area becoming limiting
and also due to their less storage ability resulting per-
haps from less involvement of the leaves in metabolite
supply to the developing seeds. In wheat, the stored meta-
bolite level in the leaves might play a critical role in
inducing branch development. Furthermore, according to Kelly
and Davies (182) shifting in nutrient partitioning occurs
during flowering when the leaves become committed to the
supply of nutrients and metabolites only to the reproduc-
tive parts, depriving the other vegetative parts including
roots, and thereby hastening the senescence process of the
vegetative parts.

One of the most interesting features of rice cultivar
is that the longevity of the whole plant could be increased
up to the senescence of tertiary branch (by about 42 days).
As there was no further development of quaternary branch
the longevity could not be further extended. The failure
of the tertiary branch to develop quaternary branch might
be attributed to the extreme reduction of leaf area in
this branch. It must be pointed out that the second leaf of
the 'mother' branch from which the alternative sink in the
form of a secondary or a tertiary branch developed always
senesced earlier, possibly due to development of a nutrient
exhaustion stress resulting from the metabolite supply  to

the 'daughter' branch. Another point of interest is that
if any senescence factor(s) was presumably produced within
the leaves during floral differentiation (when maximal
increase in genetic materials such as DNA, RNA and total
protein took place in the shoot apex), it was certainly
not transmitted to the 'daughter' branch. Had this happened,
the 'daughter' branch would have senesced much earlier than
what was observed in rice cultivars. It is also to be noted
that senescence of photoperiod-sensitive rice cultivars,
such as Kalojira, Badsabhog, Patnai and Kalma (Table 48),
could be enhanced substantially (about six months) if grown
in the field under unfavourable photoperiodic conditions.
A number of reports showed that the senescence of monocarpic
plants could be prevented almost indefinitely if the flower-
ing could be prevented by subjecting the plants to unfavou-
rable conditions (64,77,307,432).

If all these facts are taken together, there seems to
be no other alternative but to conclude that the genes res-
ponsible for inducing senescence are perhaps expressed in
the leaf at the time of flowering itself in monocarpic plants.
The male hemp plant (Cannabis sativa L.), without fruits,
senesced almost at the same time as the female plant bear-
ing fruits. This was also true in spinach (Spinacea oleracea).
Thus, in these plants flowering and not the fruiting is the
main criterion for inducing senescence of the whole plant.

Furthermore, it was also reported by Kulkarni and Schwabe
(193) that senescence factor might be produced in the leaves
of Kleinia articulata. And this might also happen in cereal
species. Nevertheless, the ultimate manifestation of senes-
cence syndrome may differ somewhat in different species.
Sabater (351) has suggested that the transition from a hor-
monal equilibrium retarding senescence to another equilibrium
accelerating senescence may be triggered by genes, including
a marked change in the supply or in the synthesis of an in-
dividual hormone. Nonetheless, the exact mechanism of expre-
ssion and the location of the gene(s) remained to be explored
and a great deal of further work at the molecular level  is
needed to resolve the problems pertaining to this programmed
self-destructive process of monocarpic plants.

# S U M M A R Y

The mechanism of monocarpic senescence has been dealt
with at length as would be evident from the overwhelming
number of research publications. Nonetheless, the exact
mechanism of monocarpic senescence is not clearly understood
as yet. The present investivation aims at analysing the
possible mechanism of monocarpic senescence employing diff-
erent cultivars of rice (<u>Oryza</u> <u>sativa</u> L) and wheat (<u>Triticum</u>
<u>aestivum</u> L), viz. short-statured, photoperiod-insensitive
rice cultivars - Rasi and Sashyasri; medium-statured, photo-
period-sensitive cultivars - Kalojira and Badsabhog; tall-
statured, photoperiod-sensitive cultivars - Patnai and Kalma;
and wheat cultivars - Sonalika and Kalyansona.

The patterns of leaf senescence in all these cultivars
were studied in order to get an insight into the correlative
control and possible cause of monocarpic senescence in rice
and wheat plants. To analyse the cause of different patterns
of senescence in these cultivars, and to explore the possi-
ble role of mobilization of metabolites from leaves in the
development of these senescence patterns,some physiological,

biochemical, anatomical and hormonal studies were carried
out in intact as well as surgically altered cultivars of
rice and wheat. The study was conducted during the progress
of reproductive development of these cereals passing through
different stages, such as anthesis (0 day after anthesis or
0 DAA), grain-filling (7 DAA), grain development (14 DAA),
grain maturation (21 DAA) and senescent stage (28 DAA). In
most of the studies the decline in chlorophyll and protein
was taken as indicators of senescence development. The im-
portant findings are summarised below.

The data of the levels of chlorophyll and protein and
the percentage of yellowing patches in the flag, second and
third leaf revealed that short-statured Rasi and Sashyasri
rice cultivars displayed a non-sequential mode of leaf
senescence behaviour where the youngest flag leaf senesced.
earlier than the ontogenetically older second leaf. On the
other hand, the medium-statured Kalojira and Badsabhog rice
and Sonalika and Kalyansona wheat cultivars showed a sequen-
tial mode of leaf senescence behaviour where the leaves
senesced strictly according to their chronological age.
However, the tall-statured Patnai and Kalma rice cultivars
could be placed in between sequential and non-sequential
mode of leaf senescence (intermediate type) where both the
flag and second leaf senesced almost simultaneously.

The data of the loss of nitrogen and phosphorus, the two most mobile elements in plants, from the three uppermost leaves of these cereal cultivars revealed that it was strictly according to the mode of senescence as displayed by each of the above cultivars. The data of mobilization of $[^{32}P]$-phosphate from leaves to the grains and its retention capacity by the fed-leaf revealed that the export pattern of this isotope varied among species and cultivars. However, the export of $[^{32}P]$-phosphate to the grains was always higher in rice than that in wheat. In rice cultivars, the export of this isotope from the leaves was directly proportional to the sink strength (panicle weight) which was greater in the tall-statured cultivar. The export of $[^{32}P]$-phosphate from leaves to the grains gradually increased, reaching the maximal point at the grain development stage (14 DAA), declining thereafter. When calculated on per unit leaf area basis, the maximal export of $[^{32}P]$-phosphate was found to take place from the flag leaf of Rasi. In Kalojira and Patnai the difference in the export of radioisotope from the flag and the second leaf was not so significant. The data also revealed that the export of $[^{32}P]$-phosphate was inversely proportional to the leaf area. Thus, the maximal export took place from Rasi cultivar with maximal leaf senescence and minimal export took place in Patnai with maximal leaf area. The export pattern of radiophosphate from Sonalika wheat was similar to that of Kalojira rice

cultivar. In general, the retention capacity of $[^{32}P]$-phosphate decreased gradually with progress of reproductive development in both rice and wheat cultivars. The retention capacity of labelled phosphate followed the same trend as that of leaf senescence in both rice and wheat cultivars. When the isotope was fed through the roots and measured in the leaves and seeds, it was observed that the transport of $[^{32}P]$-phosphate gradually decreased with the progress of reproductive development in all the cultivars. The extent of transport of labelled phosphate was always greater in rice than in wheat. The export of $[^{32}P]$-phosphate was again proportional to the senescing condition of the leaf, i.e. the more was the leaf approaching senescence, the lesser was the export of radiophosphate from the roots.

Analysis of the xylem parameters at the juncture of leaf lamina and leaf sheath as well as the data of leaf area indicated a clear correlation between these parameters and the pattern of leaf senescence. Thus, in the non-sequential Rasi rice cultivar, the leaf area and xylem parameters, such as the number of vascular bundles at the juncture of leaf lamina and leaf sheath, the area of xylem vessels in a bundle and the area of lumen of the largest vessel, were approximately double in the second leaf than in the flag. In the sequential Kalojira rice cultivar, such parameters were almost equal in both flag and second leaf, whereas

in the intermediate Patnai rice and Sonalika wheat culti-
vars, these were marginally greater in the second than in
the flag leaf.

External application of BA (benzyladenine, $4.4 \times 10^{-4}$ M),
$GA_3$ (gibberellic acid, $2.9 \times 10^{-4}$ M) and their combination
($BA + GA_3$) significantly delayed leaf senescence, the effect
being most pronounced with ($BA + GA_3$), followed by separate
application of BA and $GA_3$. However, such treatments did not
alter the mode of senescence displayed by each cultivar.
ABA (abscisic acid, $7.5 \times 10^{-5}$ M), on the other hand, promoted
leaf senescence in all the cultivars and also did not alter
the mode of leaf senescence. The loss of nitrogen and phos-
phorus from the leaves of rice and wheat cultivars was
inhibited by BA, $GA_3$ and ($BA + GA_3$) treatment but it was
promoted further by ABA treatment. BA treatment also enhanced
retention capacity of $[^{32}P]$-phosphate of the fed leaf and
also the export from leaves to grains in all the cereal
cultivars, whereas ABA acted in an opposite manner. Although
BA enhanced the export of $[^{32}P]$-phosphate, it delayed sene-
scence. Whereas ABA decreased $[^{32}P]$-phosphate export but
promoted senescence.

An analysis of the changes in histone protein and RNA
in leaves of rice and wheat cultivars revealed that with
the approach of senescence there was a decline in RNA and
rise in histone protein. And there was also a consistent

decline in RNA:histone ratio. While BA increased RNA
synthesis, raised RNA:histone ratio and decreased histone
protein, ABA decreased RNA, lowered RNA:histone ratio and
increased histone protein in all the leaves of cereal cul-
tivars with ageing and senescence.

Concomitant with the decrease in protein level, there
was a rise in protease activity and free amino acid accumu-
lation in the leaves which were proportional to the ageing
and senescing condition of the leaf. Treatments with BA and
ABA produced an inhibitory and promotive effects, respec-
tively, on these parameters.

There was a senescence-related proportional increase
in malondialdehyde (MDA) content, (which is an oxidation
product of polyunsaturated membrane fatty acids and a
reliable indicator of membrane deterioration) in leaves
of different rice and wheat cultivars suggesting that the
loss of membrane integrity is a function of ageing  and
senescence in these cultivars. That such membrane deterio-
ration is induced by free radicals could be indirectly
substantiated from the observations of the decline in the
activities of superoxide dismutase (SOD) and catalase in
leaves with approaching senescence, and such a decline
possibly favoured free radical accumulation and induced
membrane deterioration. The rise in peroxidase activity
during senescence of leaves of these cultivars might also

facilitate oxidative degradation of cellular macromolecules. The accumulation of MDA and changes in free radical scavenging enzymes were proportional with ageing in rice and wheat cultivars. External application of BA significantly retarded MDA accumulation and increased SOD, catalase and peroxidase activities. ABA application, on the contrary, produced an opposite effect.

The rate of transpiration either by the whole plant or by an individual leaf, generally taken as an indicator of stomatal opening and closing as well as capacity for uptake of cytokinins, nutrients and water from roots to aerial parts, gradually decreased during the reproductive development of rice and wheat cultivars with the concomitant increase in proline accumulation. In Rasi, the decline in the rate of transpiration and rise in the accumulation of proline were greater in the flag leaf than in the second leaf at the senescent stage; whereas in Kalojira rice and Sonalika wheat cultivars the sequence of these events occurred according to the chronological age of the leaf. Foliar application of BA enhanced transpiration rate and also suppressed proline accumulation, whilst ABA application gave an opposite effect.

In order to assess the role played by senescence retarding and promoting hormones in whole plant senescence, the endogenous levels of cytokinin-like (CK-like) substances

and ABA and the release of ethylene from the leaves were
measured with the progress of reproductive development of
rice and wheat cultivars. The CK-like substances and the
ratio between CK-like substances and ABA gradually decreased,
while ABA and ethylene increased with the progress of re-
productive development. The level of CK-like substances was
in general higher in rice than in wheat. In the Rasi rice
cultivar, CK-like substances and the ratio between CK-like
substances and ABA was greater in the second leaf than in
the flag leaf at the senescent stage. An opposite trend was
noticed in Kalojira rice and Sonalika wheat cultivars. The
level of ABA gradually increased in all the leaves of rice
and wheat cultivars, reaching the maximal level at the
grain maturation stage (21 DAA), declining thereafter. The
release of endogenous  ethylene was higher in the flag and
second leaf at the anthesis stage (0 DAA), followed by a
decline up to the grain development stage (14 DAA) and a
rise thereafter.

There was an increase in the content of total protein
and nucleic acids in the shoot apex 9-12 days before panicle
emergence in all the cereal cultivars studied. After that,
there was a decline in the content of these macromolecules,
with the concomitant rise in the content of histone protein.
These results indicated that marked changes in the genetic
materials, as manifested by the changes in nucleic acids

and both acidic and basic proteins, occurred in the shoot
apex of these cereal cultivars prior to transition from
the vegetative to the reproductive stage.

Reproductive parts of monocarpic plants are important
agents which influence the whole plant senescence presuma-
bly by drawing metabolites from the vegetative parts and/or
supplying some yet unknown senescence factor(s) to the
vegetative parts. The present experiment showed that the
removal of panicle at the anthesis (O DAA) and grain-filling
stages (7 DAA) markedly delayed the leaf senescence of all
cultivars studied. Such treatments also altered the mode of
leaf senescence from non-sequential to sequential in only
Rasi rice cultivar possibly due to development of an alter-
native sink at the second leaf axil. Although such treatment
delayed senescence in wheat cultivar, the effect was much
less pronounced compared with that of rice cultivars. The
extent of senescence delaying effect diminished as the act
of surgical removal of the panicle was delayed. Thus, such
treatments at the grain development (14 DAA) and grain
maturation (21 DAA) stages had no effect on the retardation
of leaf senescence and could not alter the mode of leaf
senescence even in Rasi as there was no development of
alternative sink. The delaying effect due to panicle removal
was greater in rice than in wheat. One of the possible
reasons of such difference might be ascribed to greater

availability of current photosynthate produced by the glumes in wheat than in rice, making the former less dependent on the source leaf unlike that in rice. Thus the content of chlorophyll and protein of glumes was significantly higher in wheat than in rice at the earlier stages, while the decline was greater in wheat than in rice during the later stages of reproductive development.

The analysis of nitrogen and phosphorus contents of the leaves of rice and wheat cultivars from which the panicle was removed at the anthesis (O DAA) and the grain-filling (7 DAA) stages showed that their contents decreased relatively slowly as compared with that of the intact control plants with the progress of reproductive development. The removal of panicle at the grain development (14 DAA) stage could neither reduce the loss of nitrogen and phosphorus nor delay the senescence suggesting that the maximal sink demand possibly was developed around the grain development stage (14 DAA) which caused the greatest depletion of nutrients and subsequently enhanced senescence. When the panicle was removed at the grain development stage (14 DAA) or at the later stages, there was no change in the mineral contents as well as senescence of the leaves over the intact control plants. The study with $[^{32}P]$-phosphate export from leaves also corroborated this.

The surgical excision of the flag leaf had the most significant effect on the enhancement of senescence in all the rice and wheat cultivars. While removal of the second leaf also enhanced the senescence of the flag leaf, the extent was less prominent compared with that of the second leaf when the flag leaf was removed. The removal of the third leaf had little effect on the senescence of the other two leaves. These results suggested that the flag leaf played an important role in the mobilization of metabolites in the cereal cultivars. Analysis of leaf nitrogen and phosphorus contents of the remaining leaves as well as $[^{32}P]$-phosphate retention capacity and export data of rice and wheat cultivars from which a particular leaf was excised provided further credence to the above suggestion.

In order to further clarify the role played by the reproductive structures on the senescence process of rice and wheat cultivars, attempts were made to examine the effects of removal of different percentage of spikelets from the panicle or emasculation treatment of the panicle on the whole plant senescence. The removal of 50, 75 and 100 percent spikelets from the panicle or emasculation treatment in the main-tiller of rice cultivars induced the development of secondary branch with two leaves at the axil of the second leaf. Similarly, removal of 75 and 100 percent spikelets from the panicle of the secondary

branch of rice or the emasculation treatment induced the development of tertiary branch from its second leaf axil. But such treatment on the tertiary branch could not induce further branch development in both the rice cultivars. Interestingly, such surgical treatment on wheat plant had no effect on branch development. The leaf area of the flag and the second leaf of the main-tiller, secondary branch and tertiary branch gradually decreased with the concomitant decrease in seed number.

The removal of 50, 75 and 100 percent spikelets from the panicle of the main tiller or its emasculation treatment delayed leaf senescence in both rice and wheat cultivars and altered the non-sequential mode of senescence to sequential mode in Rasi rice cultivar. However, the delaying effect of spikelet removal on senescence was greater in rice than in wheat. Similarly, 75 and 100 percent spikelet removal or emasculation treatment of the secondary branch of rice cultivars delayed leaf senescence but altered the mode of senescence only in Rasi. However, 25 and 50 percent removal of spikelets had no effect on either branch development or delaying of senescence of the secondary branch. Such treatment on tertiary branch, although delayed leaf senescence, did not alter the mode of leaf senescence in Rasi possibly due to the absence of an alternative sink in the form of a quaternary branch. It is noteworthy that

the total longevity of the main-tiller of rice (whole plant) could be extended by continuous allowance of branch development over the untreated intact control plants. Thus, in rice the failure of further branch production (quaternary) due to removal of spikelets or emasculation treatment of the tertiary branch marked the end of the whole plant longevity.

# EVENTS OF MONOCARPIC SENESCENCE IN CEREALS
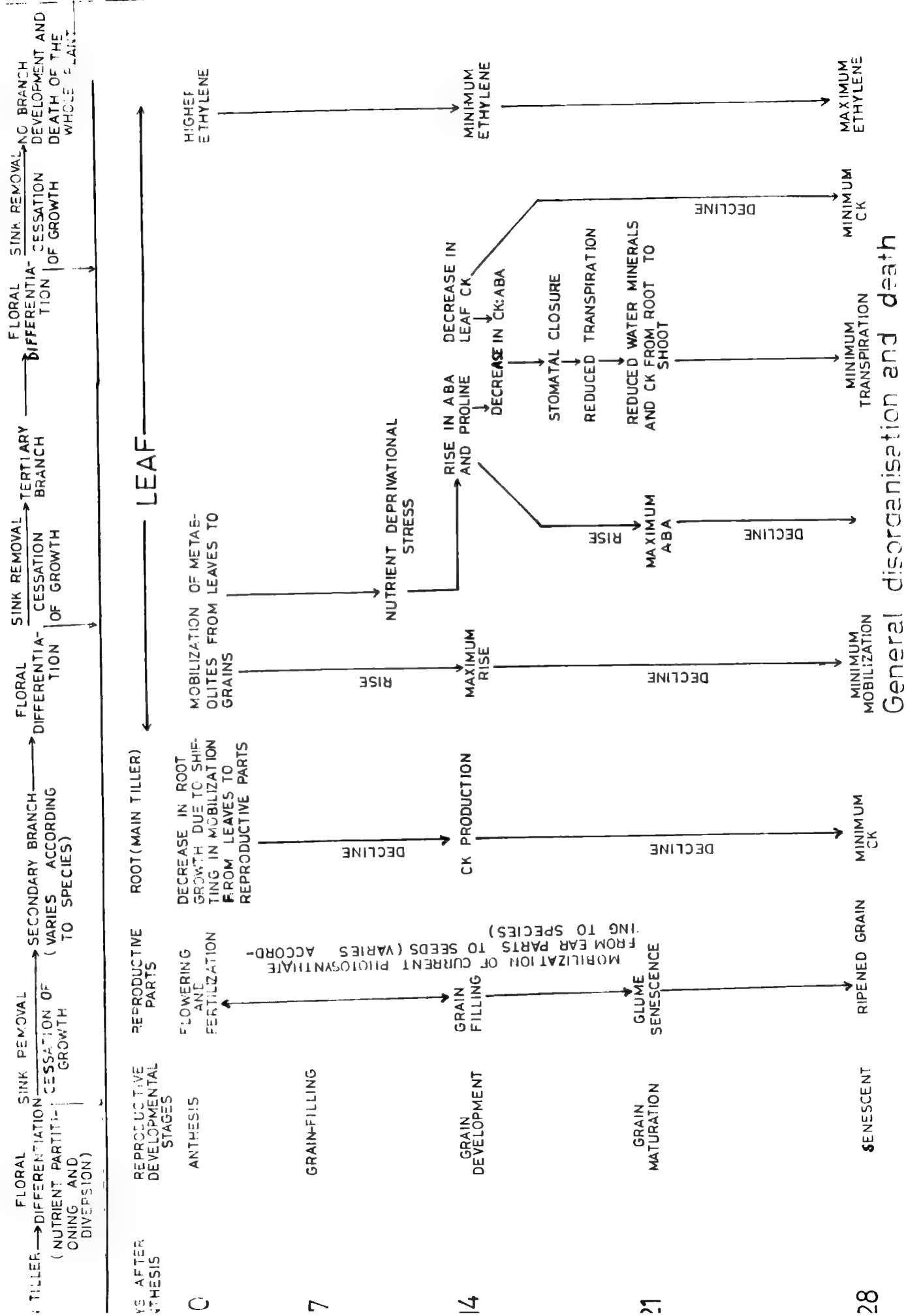
# FIGURES

# EVENTS OF MONOCARPIC SENESCENCE IN CEREALS

TILLER → FLORAL DIFFERENTIATION (NUTRIENT PARTITIONING AND DIVERSION) → SINK REMOVAL CESSATION OF GROWTH → SECONDARY BRANCH (VARIES ACCORDING TO SPECIES) → FLORAL DIFFERENTIATION → SINK REMOVAL CESSATION OF GROWTH → TERTIARY BRANCH → FLORAL DIFFERENTIATION → SINK REMOVAL CESSATION OF GROWTH → QUATERNARY BRANCH DEVELOPMENT AND DEATH OF THE WHOLE PLANT

—— LEAF ——

| DAYS AFTER ANTHESIS | REPRODUCTIVE DEVELOPMENTAL STAGES | REPRODUCTIVE PARTS | ROOT (MAIN TILLER) | LEAF | | ethylene |
|---|---|---|---|---|---|---|
| 0 | ANTHESIS | FLOWERING AND FERTILIZATION | DECREASE IN ROOT GROWTH DUE TO SHIFTING IN MOBILIZATION FROM LEAVES TO REPRODUCTIVE PARTS | MOBILIZATION OF METABOLITES FROM LEAVES TO GRAINS | | HIGHER ETHYLENE |
| 7 | GRAIN-FILLING | | | | | |
| 14 | GRAIN DEVELOPMENT | GRAIN FILLING | CK PRODUCTION DECLINE | MAXIMUM RISE — RISE | NUTRIENT DEPRIVATIONAL STRESS → RISE IN ABA AND PROLINE | MINIMUM ETHYLENE |
| 21 | GRAIN MATURATION | GLUME SENESCENCE | | DECLINE | RISE → MAXIMUM ABA → DECLINE; DECREASE IN LEAF CK → STOMATAL CLOSURE → REDUCED TRANSPIRATION → REDUCED WATER MINERALS AND CK FROM ROOT TO SHOOT; DECREASE IN CK:ABA → DECLINE | |
| 28 | SENESCENT | RIPENED GRAIN | MINIMUM CK | MINIMUM MOBILIZATION | MINIMUM TRANSPIRATION; MINIMUM CK | MAXIMUM ETHYLENE |

MOBILIZATION OF CURRENT PHOTOSYNTHATE FROM EAR PARTS TO SEEDS (VARIES ACCORDING TO SPECIES)

General disorganisation and death

Fig.1. Changes in chlorophyll content in the flag (O——O),
second (△——△) and third (□——□) leaf of six rice
cultivars during the progress of reproductive deve-
lopment. Data were recorded at intervals of 7 days
from anthesis to senescent stage of each rice cul-
tivar. Bars indicate ± SE for six replicates.
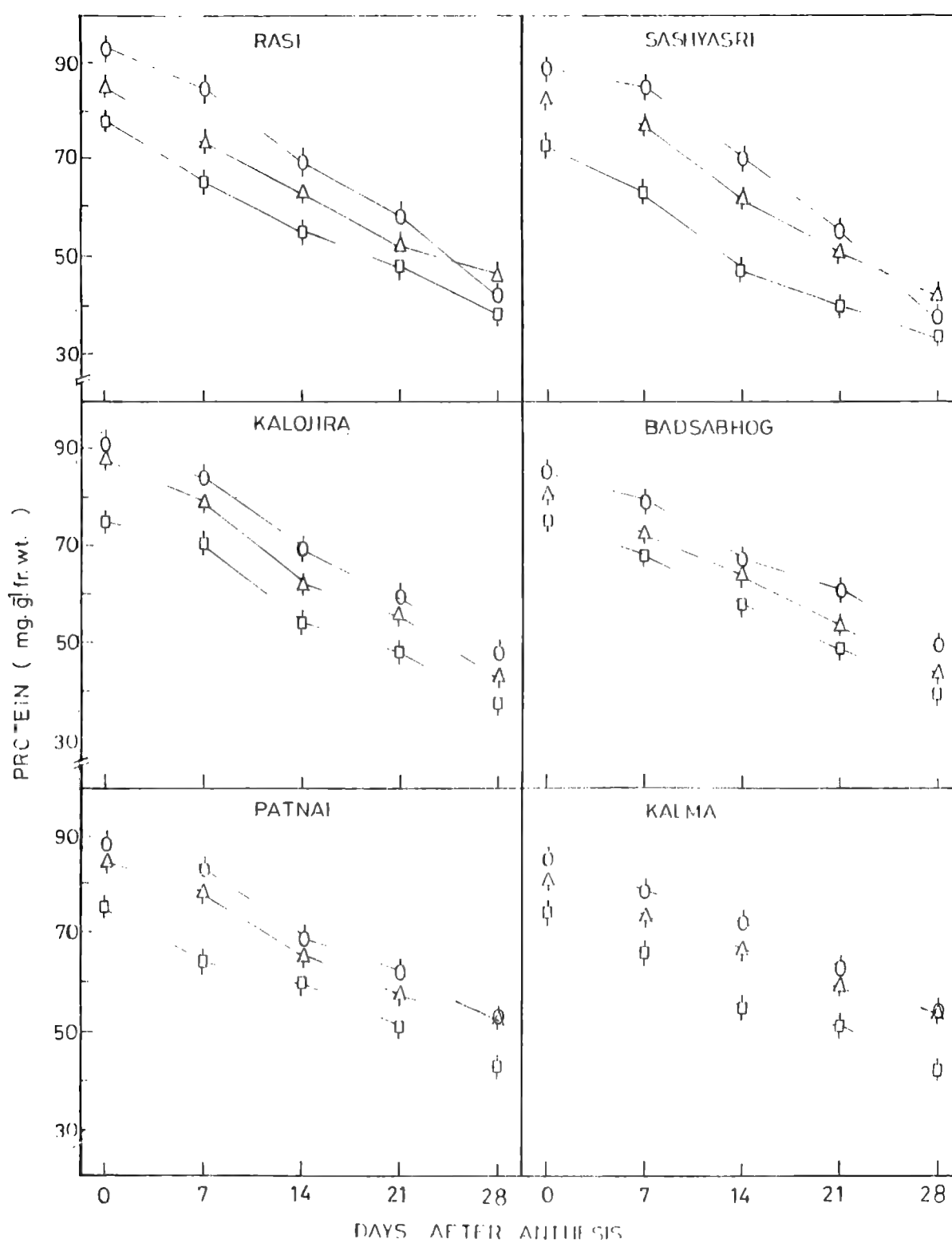
Fig.2. Changes in protein content in the flag (O——O), second (△——△) and third (□——□) leaf of six rice cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.
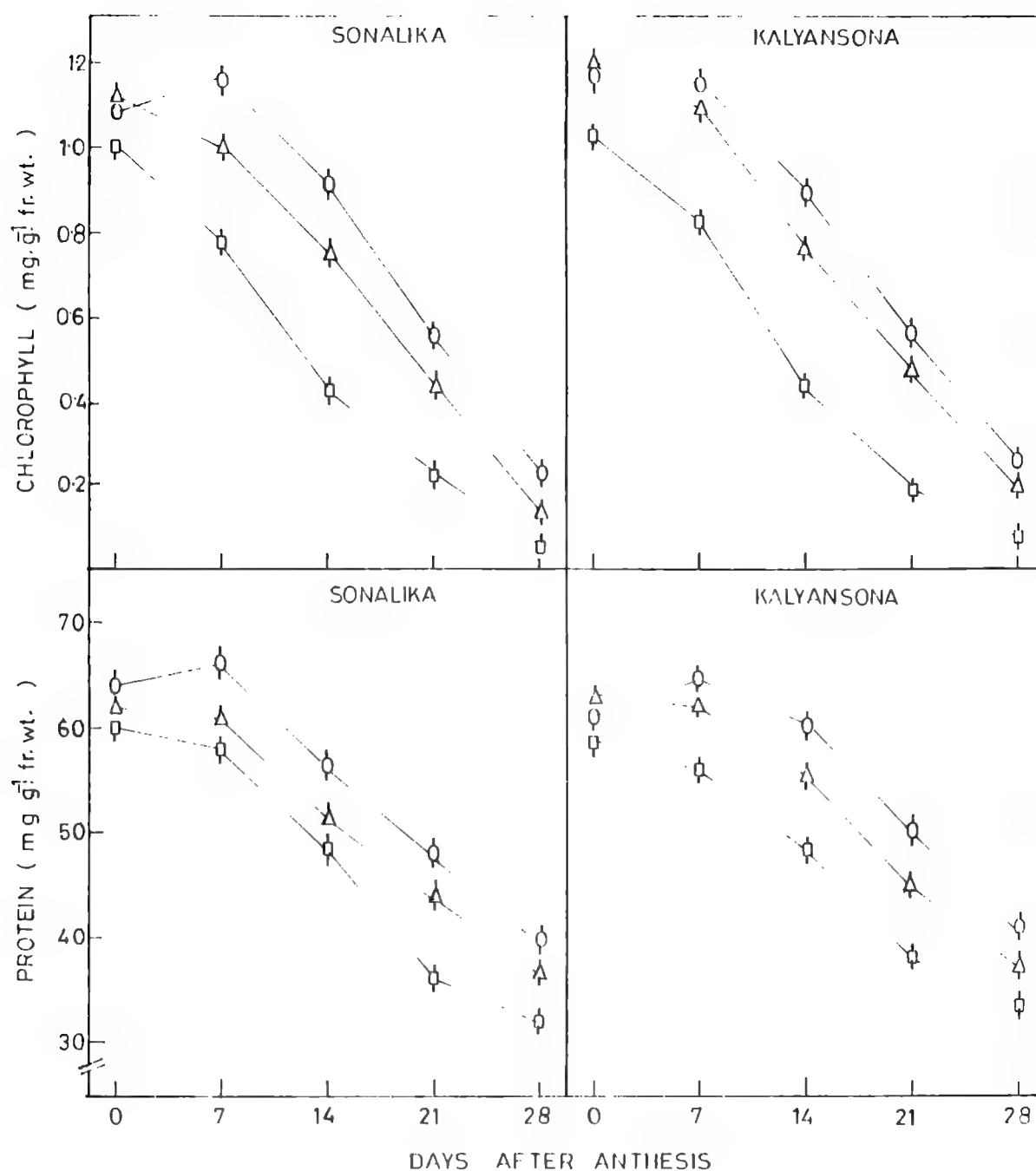
Fig.3. Changes in chlorophyll and protein contents in the flag
(o——o), second (△——△) and third (□——□ ) leaf of
two wheat cultivars during the progress of reproductive
development. Data were recorded as in Fig.1. Bars as
in Fig.1.
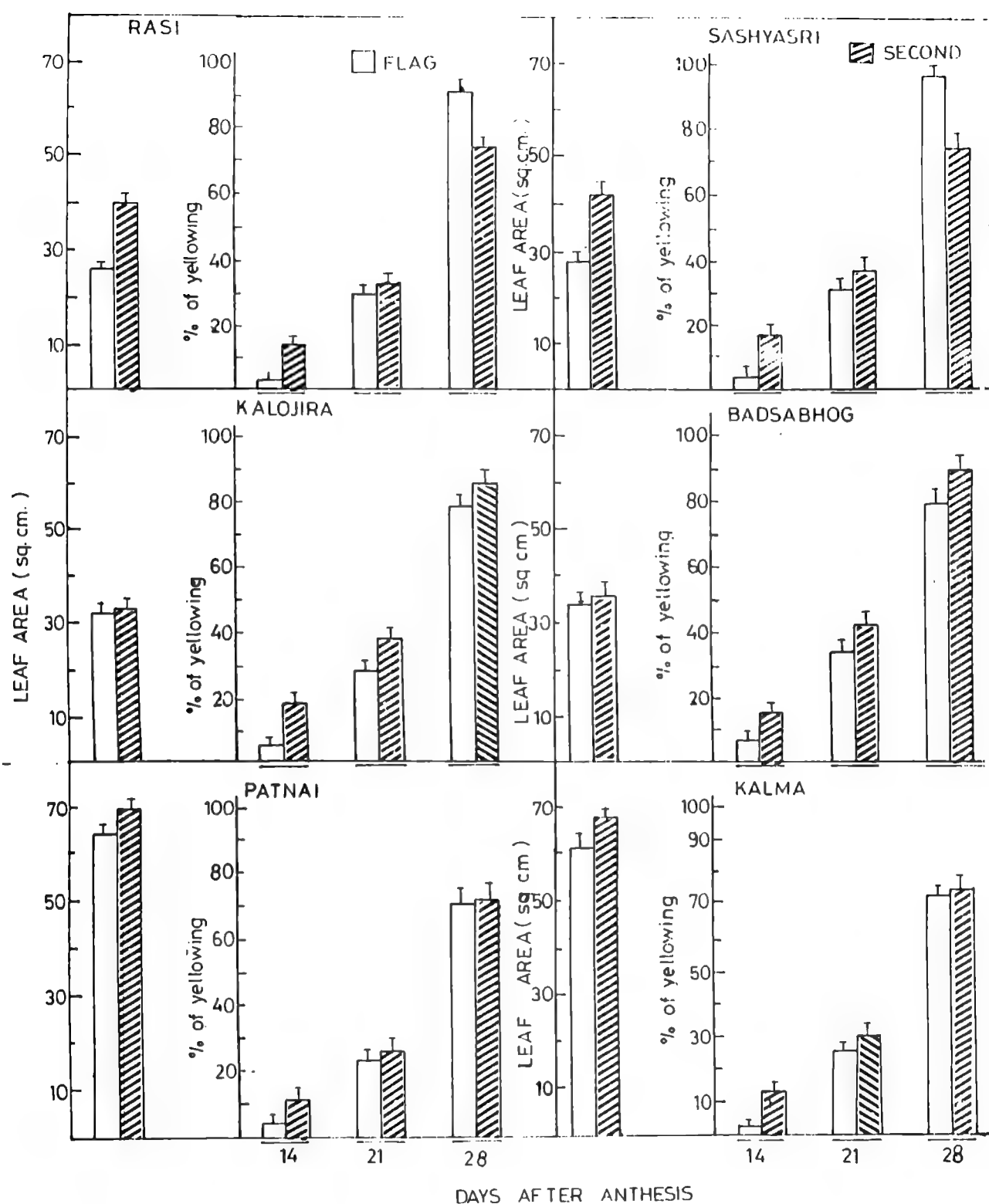
Fig.4. Total leaf area and changes in the percentage of yellowing patches (expressed as percentage of total leaf area) in the flag (☐) and second (▨) leaf of six rice cultivars. Data were recorded as in Fig.1. Bars as in Fig.1.
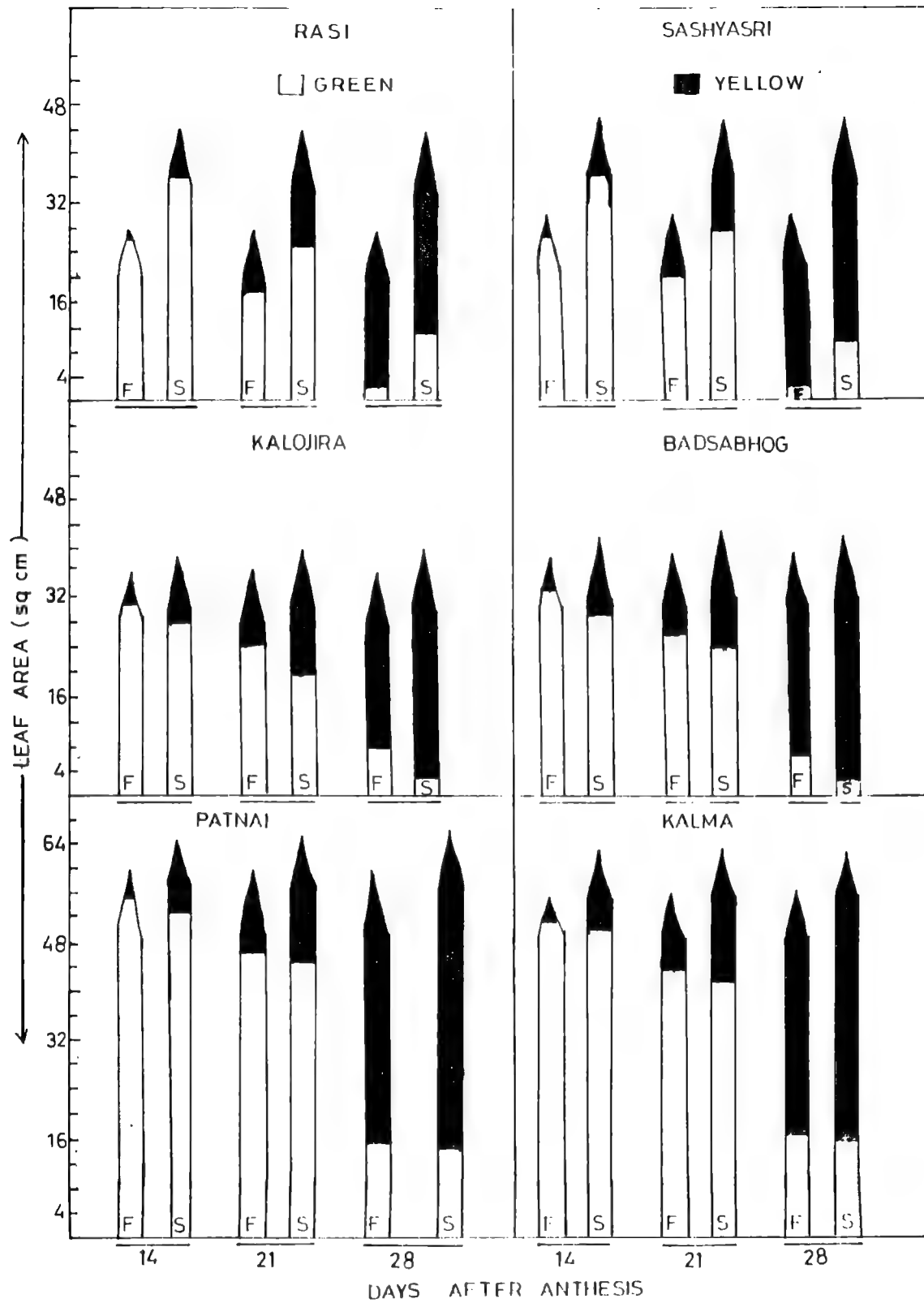
**Fig.5. Diagrammatic representation of green ( □ ) and yellow ( ■ ) area of the flag (F) and second (S) leaf of six rice cultivars during the progress of reproductive development.**
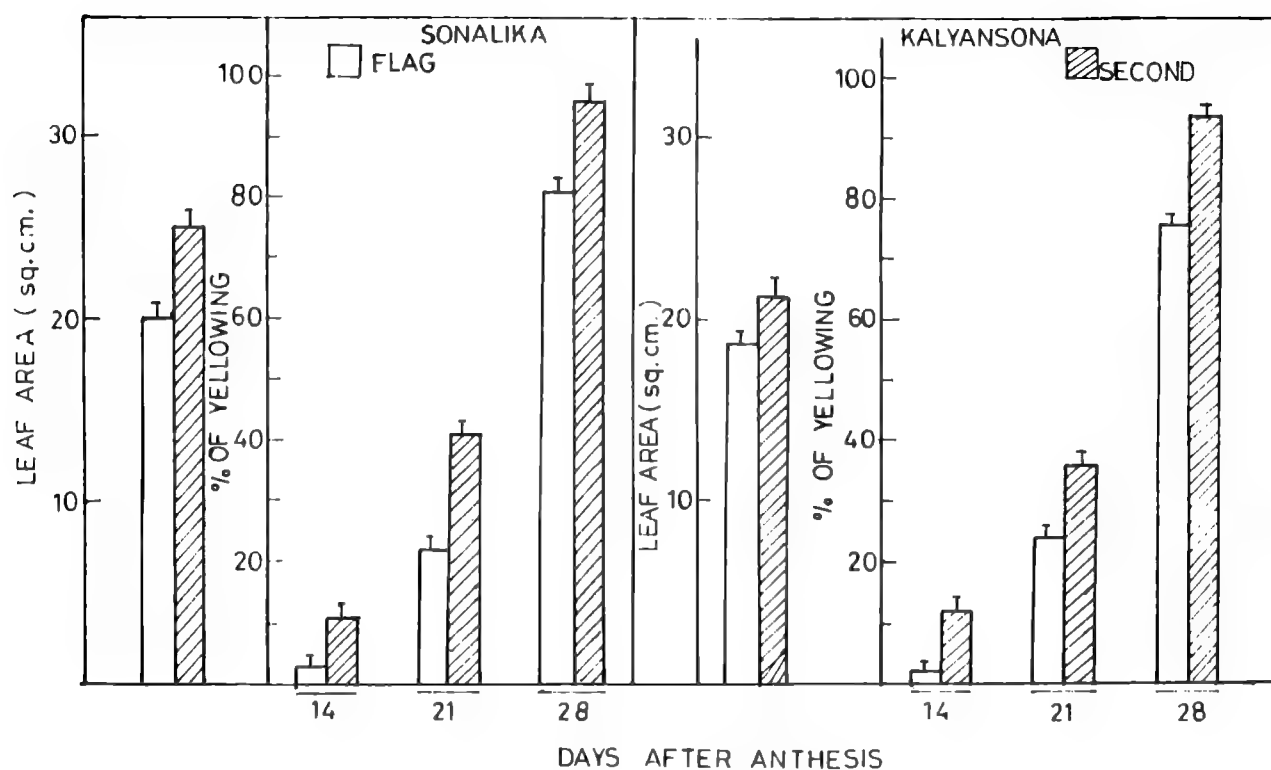
Fig.6. Total leaf area and changes in the percentage of yellow-
ing patches (expressed as percentage of total leaf area)
in the flag ( □ ) and second ( ▨ ) leaf of two wheat
cultivars. Data were recorded at intervals of 7 days
from grain development to senescent stage of each
cultivar · Bars as in Fig.1.
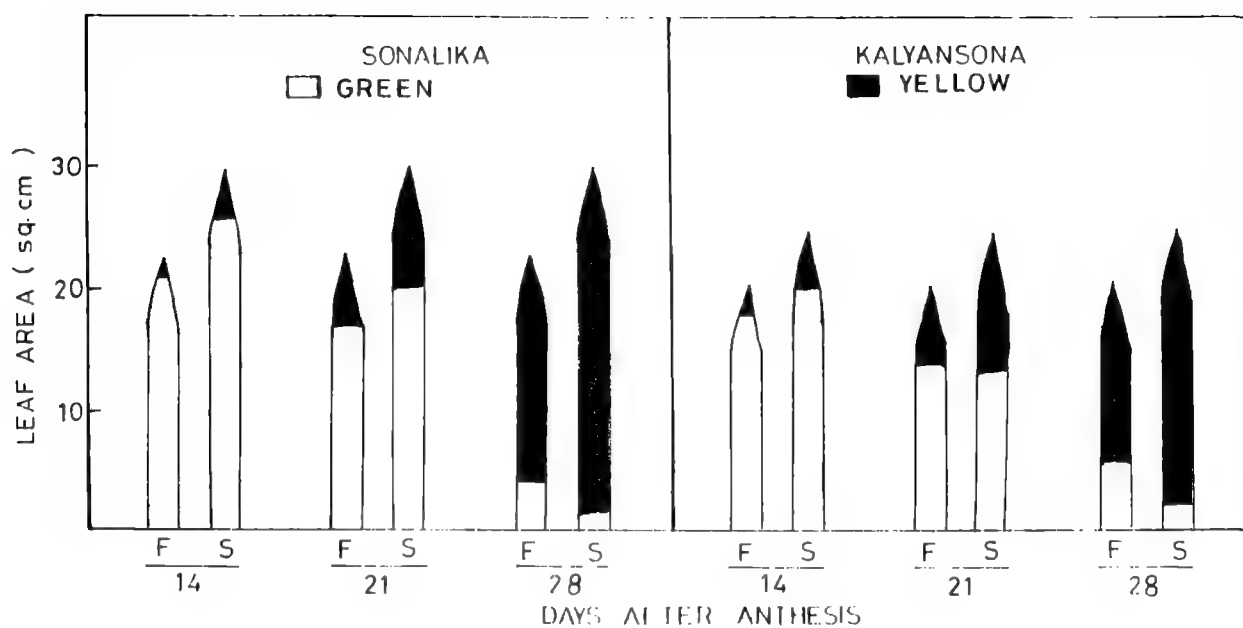
Fig.7. Diagrammatic representation of green ( □ ) and yellow
( ■ ) areas of flag (F) and second (S) leaf of two
wheat cultivars during the progress of reproductive
development.
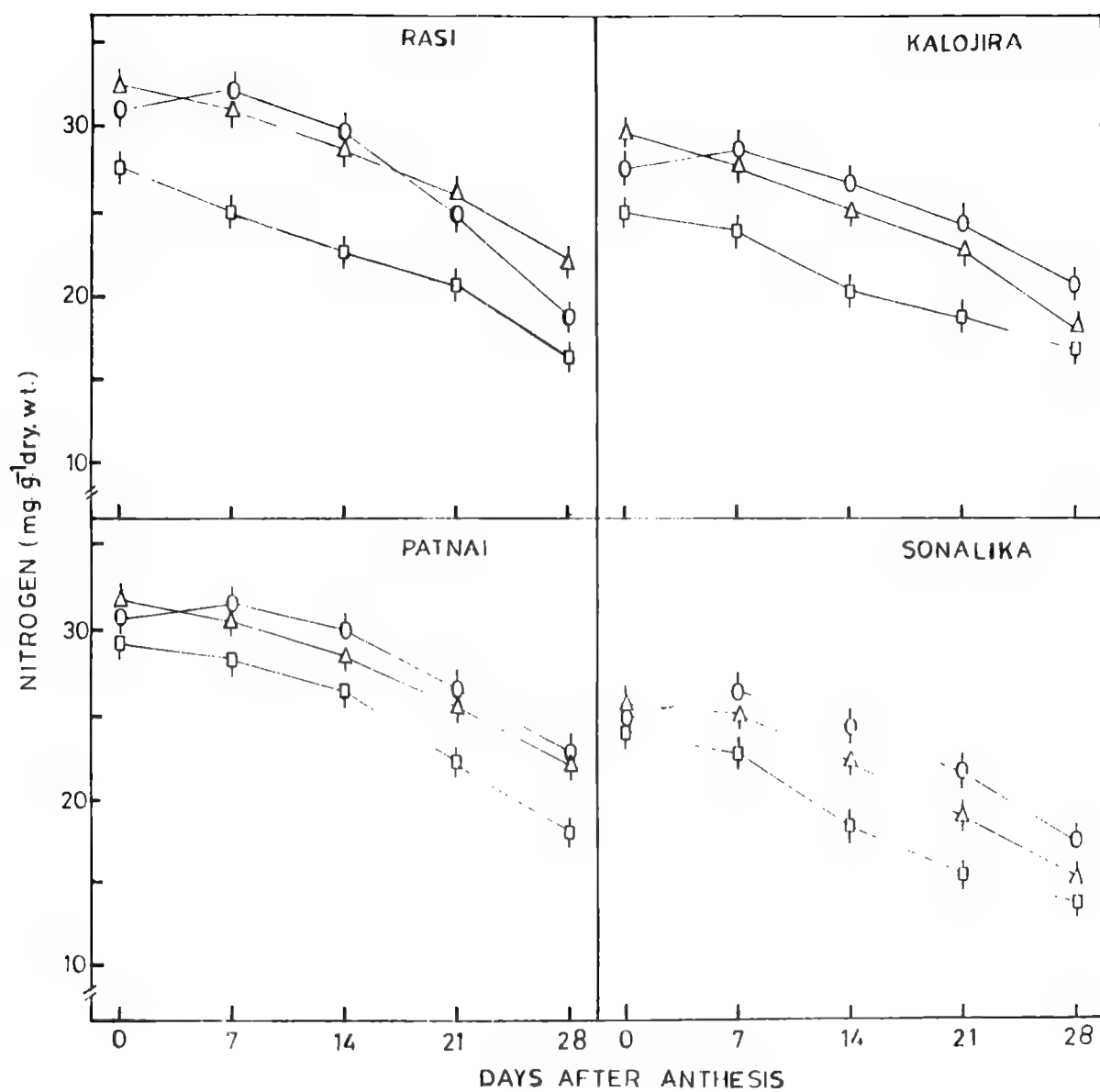
Fig.8. Changes in nitrogen content in the flag (o——o),
second (△——△) and third (□——□) leaf of three
rice and one wheat cultivars during the progress of
reproductive development. Data were recorded as in
Fig.1. Bars as in Fig.1.
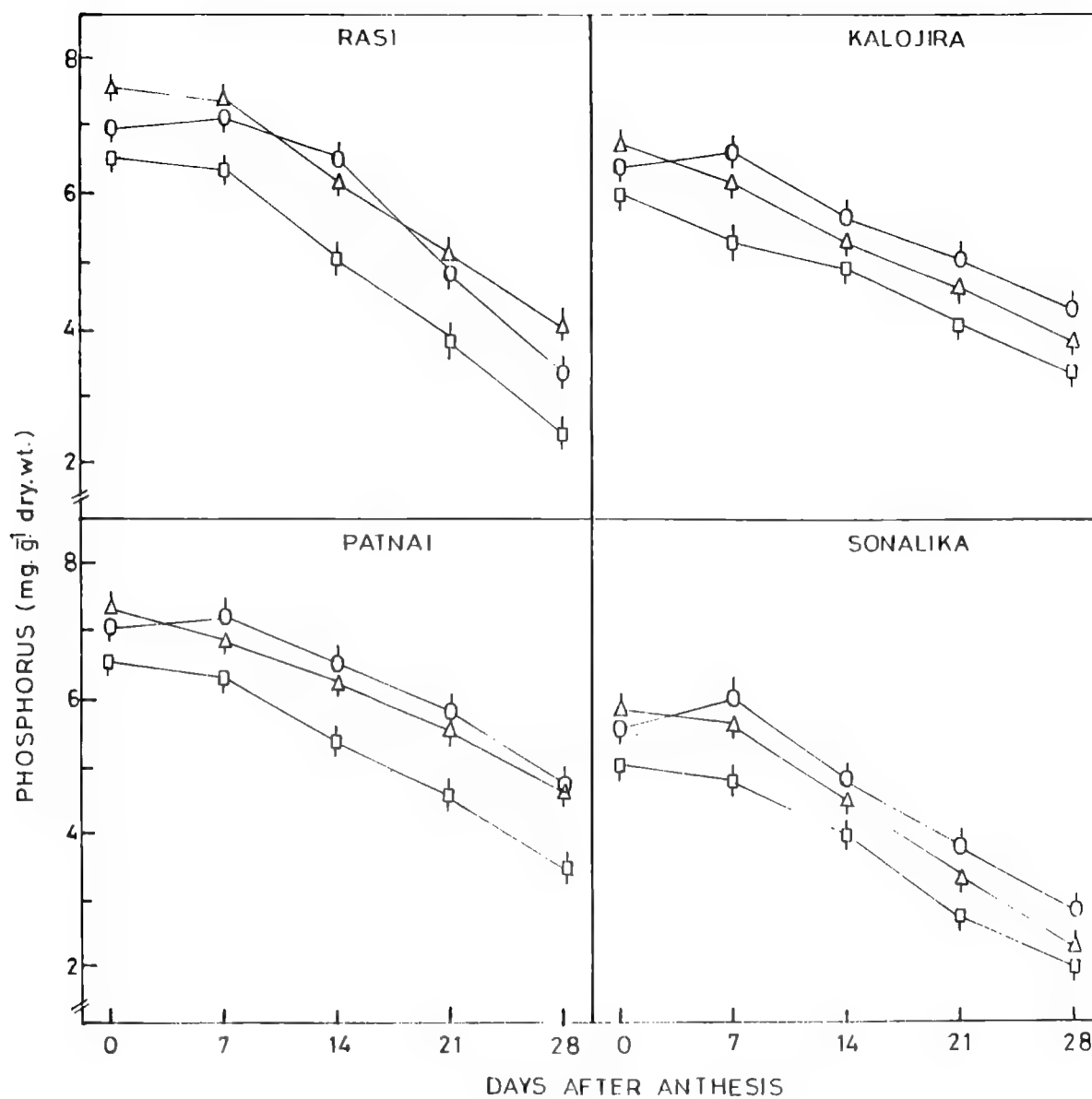
Fig.9. Changes in phosphorus content in the flag (O——O),
second (△——△) and third (□——□) leaf of three
rice and one wheat cultivars during the progress of
reproductive development. Data were recorded as in
Fig.1. Bars as in Fig.1.
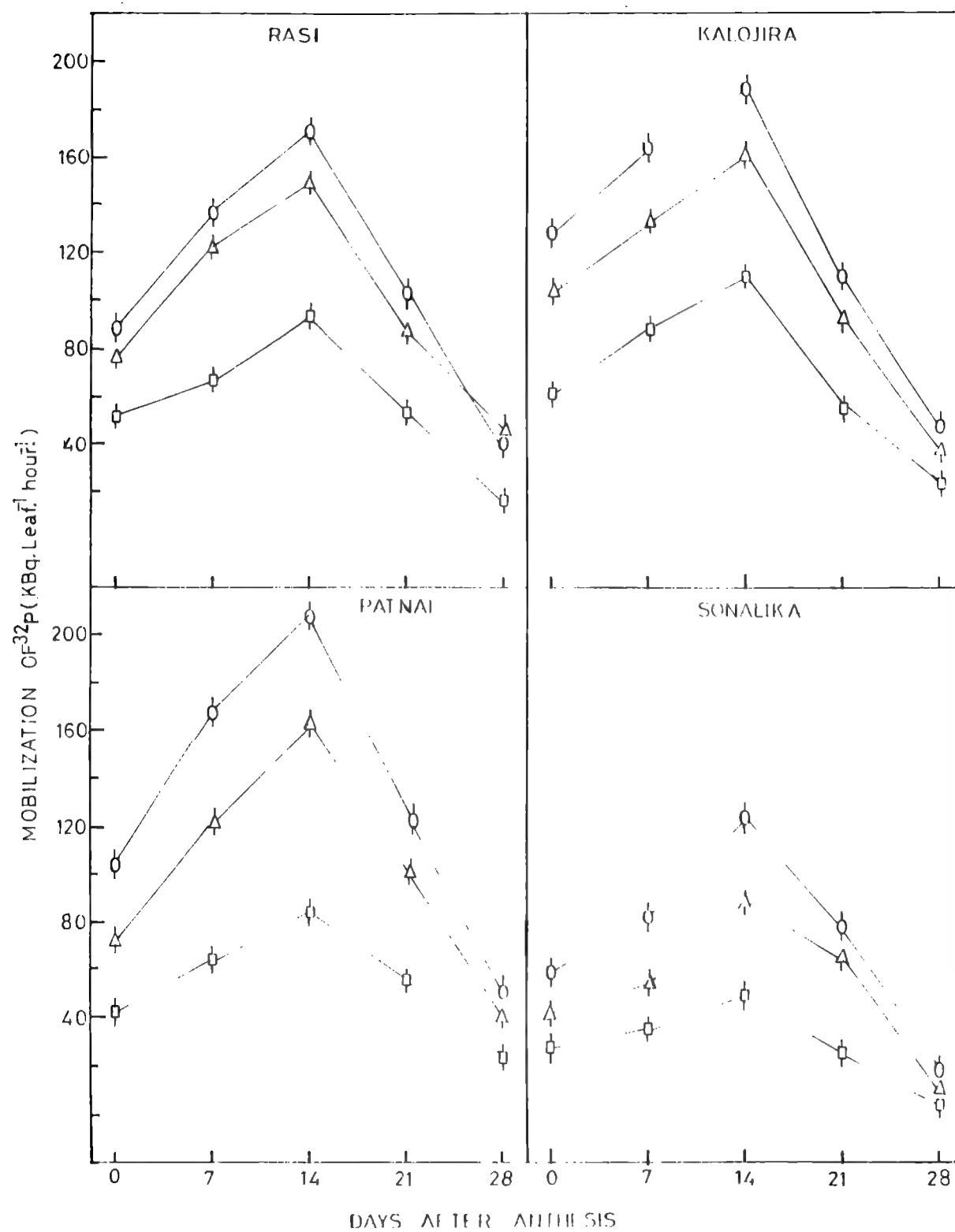
Fig.10. Changes in mobilization of [$^{32}$P]-phosphate from the whole flag (o——o), second (△——△) and third (□——□) leaf to the grains of three rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.
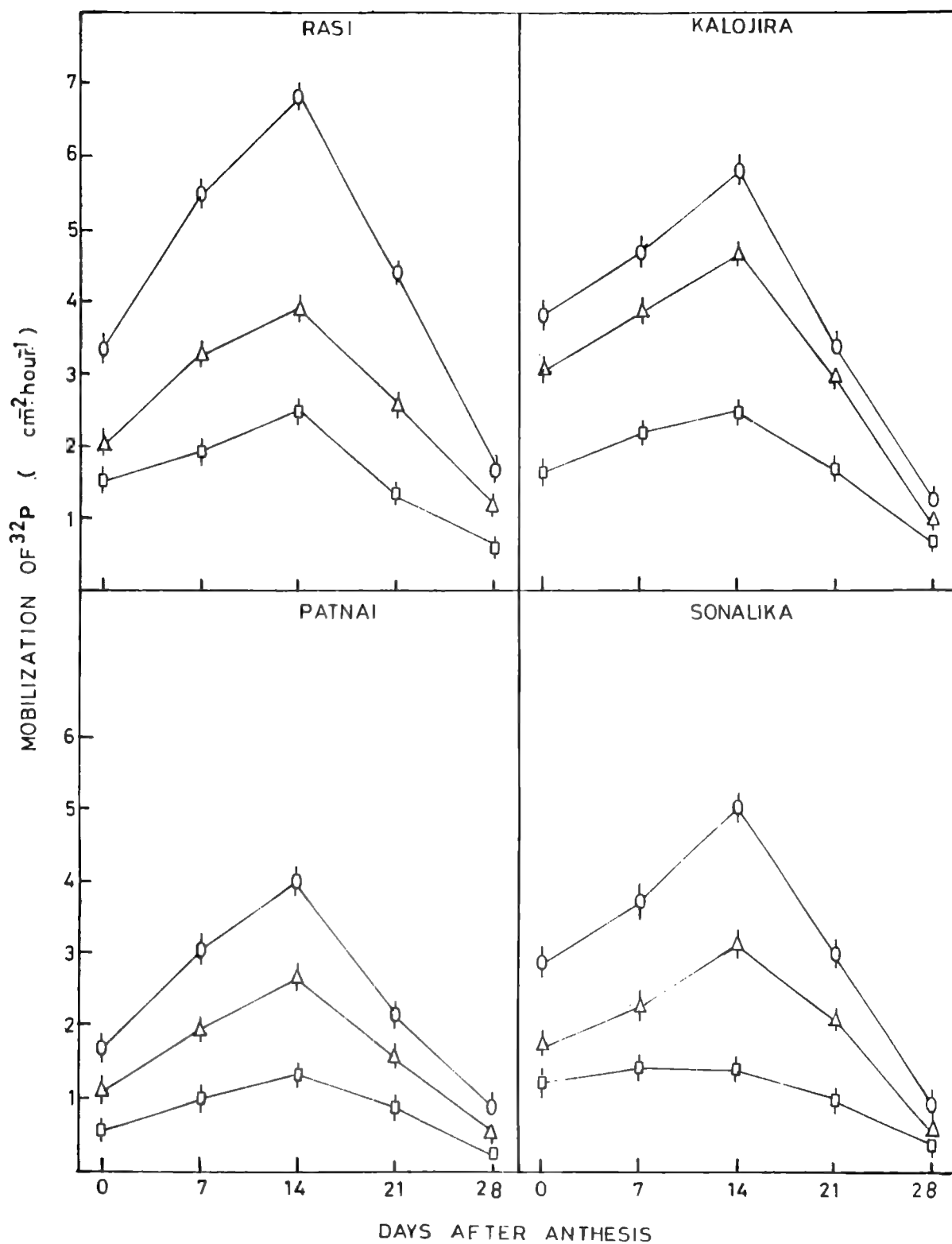
Fig.11. Changes in mobilization of [$^{32}$P]-phosphate on unit leaf area basis from the flag (o———o), second ( △———△ ) and third ( □———□ ) leaf to the grains of three rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.
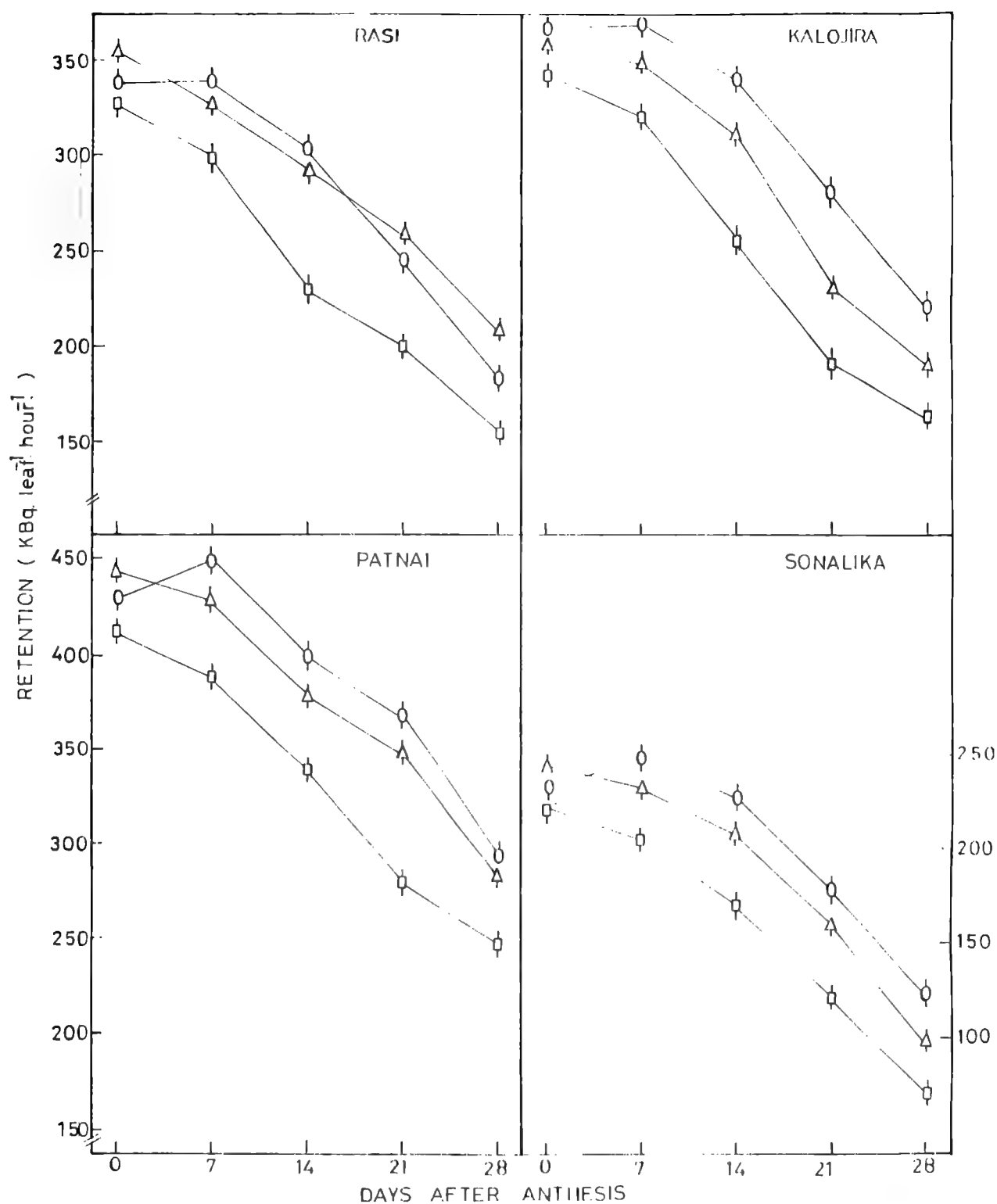
Fig.12. Changes in retention of [$^{32}$P]-phosphate in the flag
(O——O), second (△——△) and third (□——□) leaf of
three rice and one wheat cultivars during the progress
of reproductive development. Data were recorded as in
Fig.1. Bars as in Fig.1.
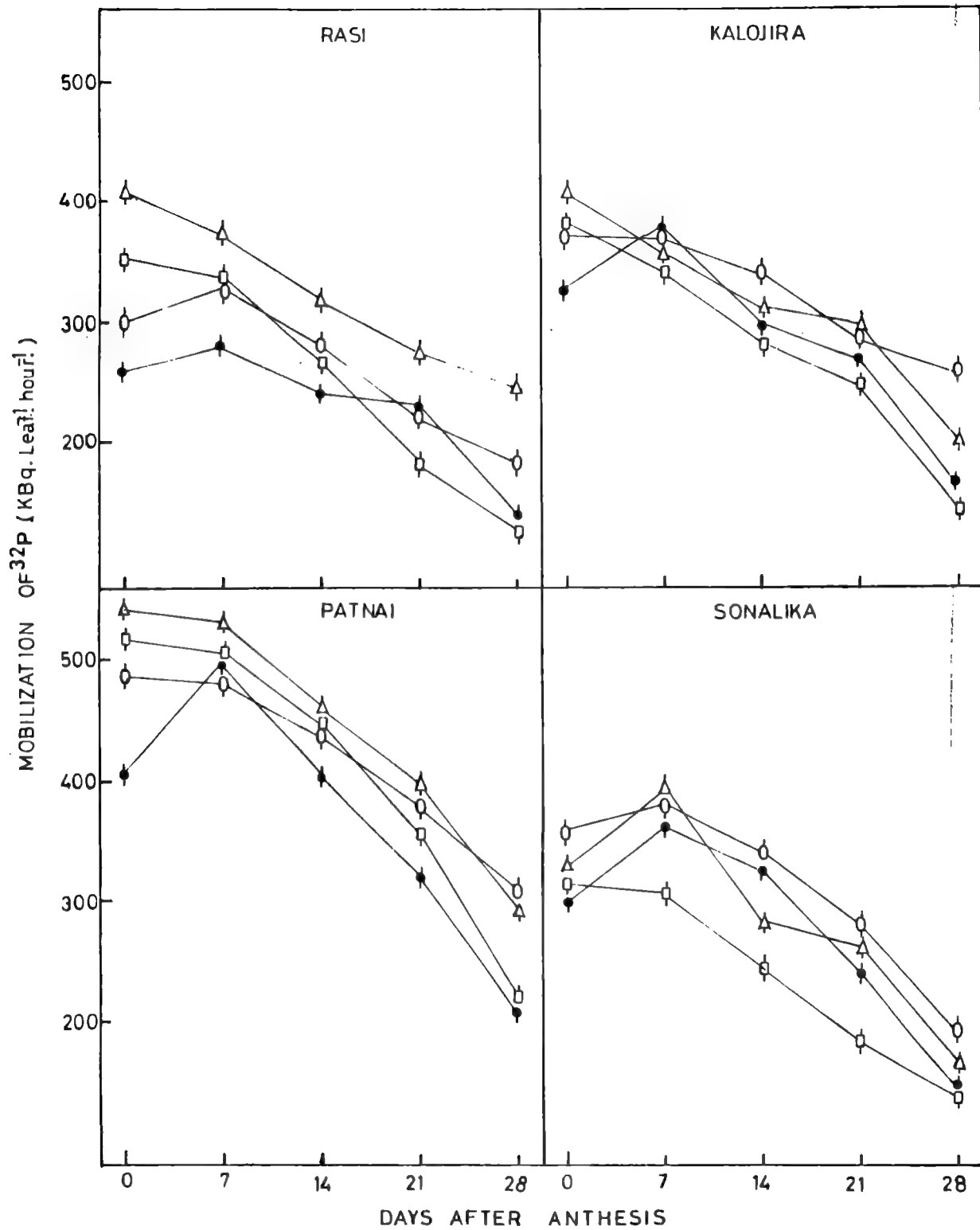
Fig.13. Changes in the export of [$^{32}$p]-phosphate from the roots to the flag (○——○), second (△——△) and third (□——□) leaf and grains (●——●) of three rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

TOTAL NUMBER OF VASCULAR BUNDLES    AREA OF VESSELS IN A BUNDLE
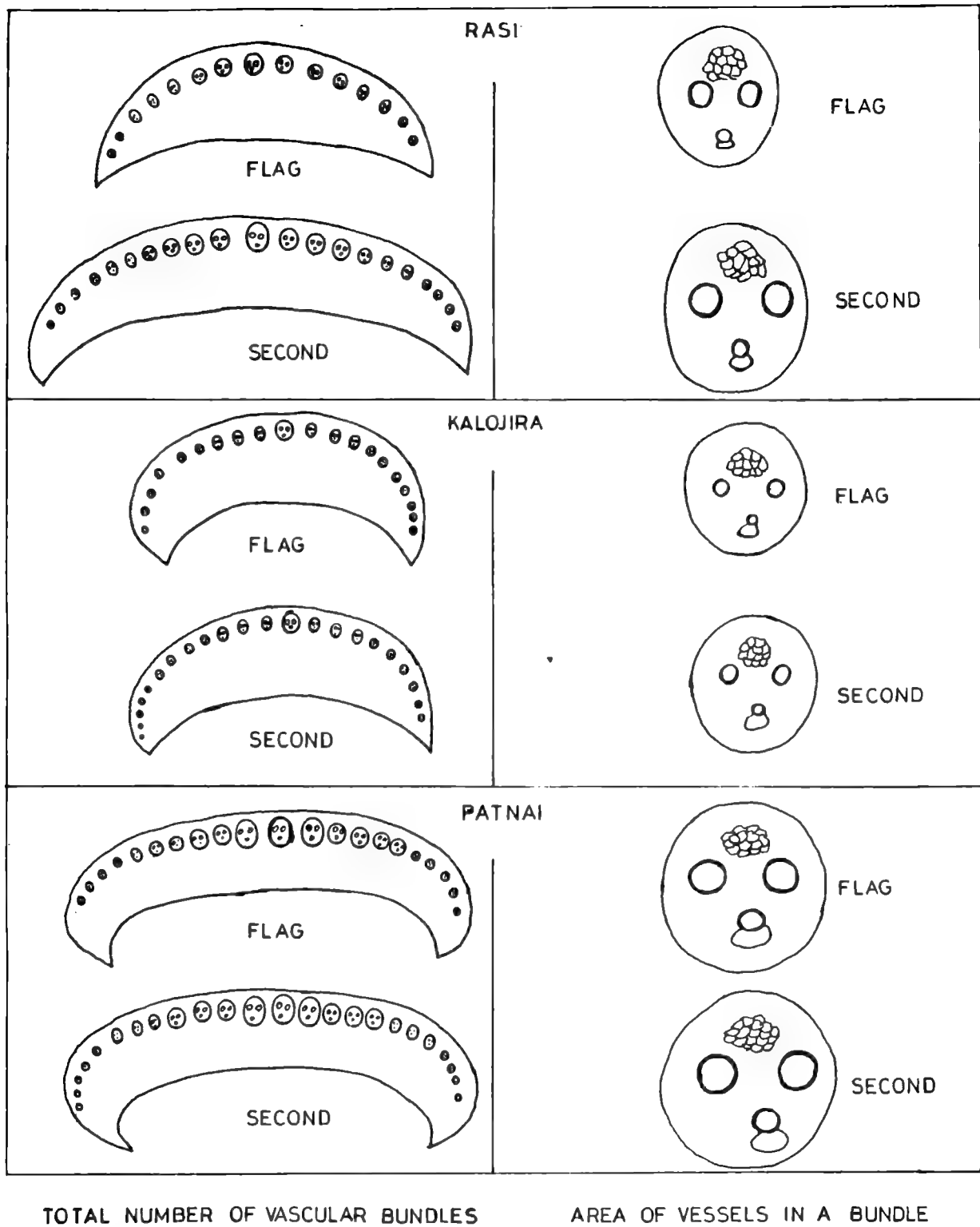
Fig.14. Diagrammatic representation of total number of vascular bundles and area of the xylem vessels in a bundle at the juncture of leaf lamina and leaf sheath of the flag and second leaf of three rice cultivars.
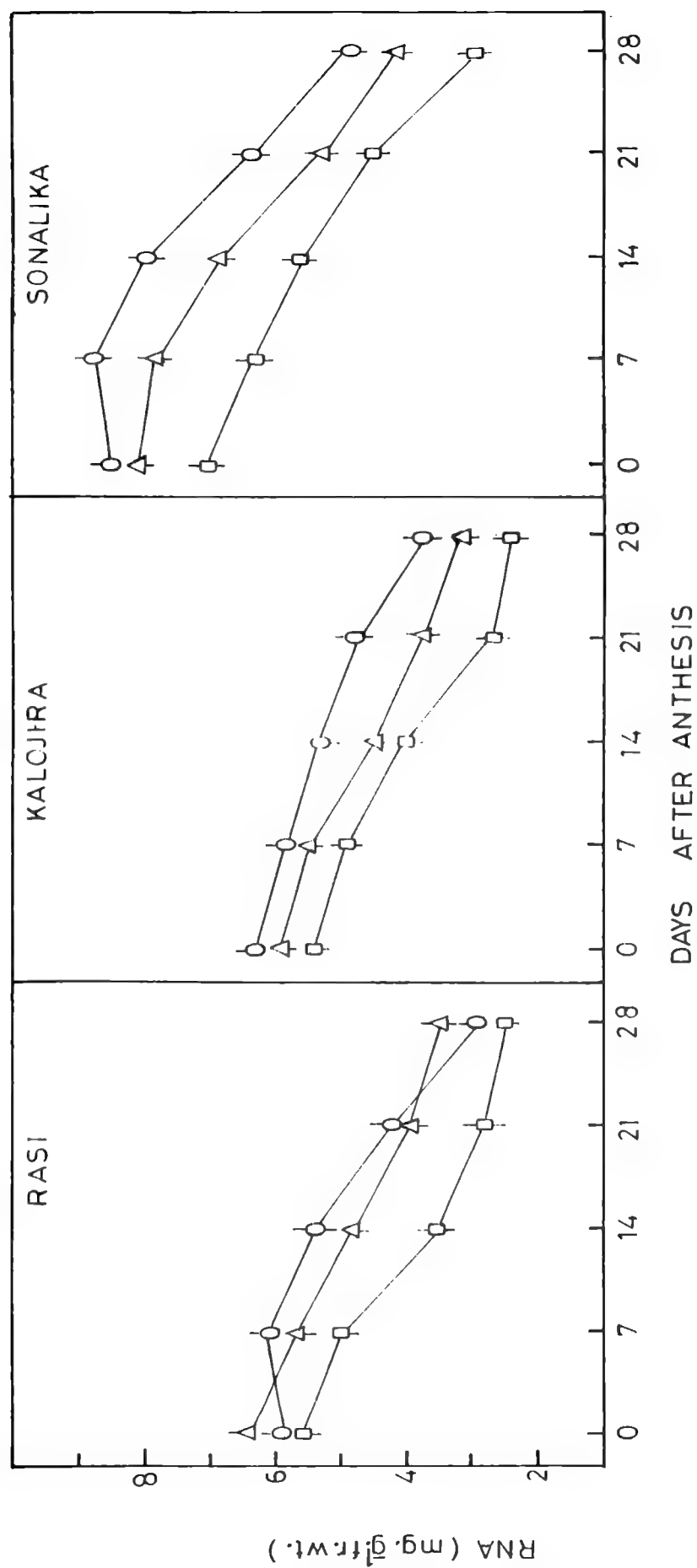
Fig.15. Changes in the contents of RNA in the flag ($\circ$——$\circ$), second ($\triangle$——$\triangle$) and third ($\square$——$\square$) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.
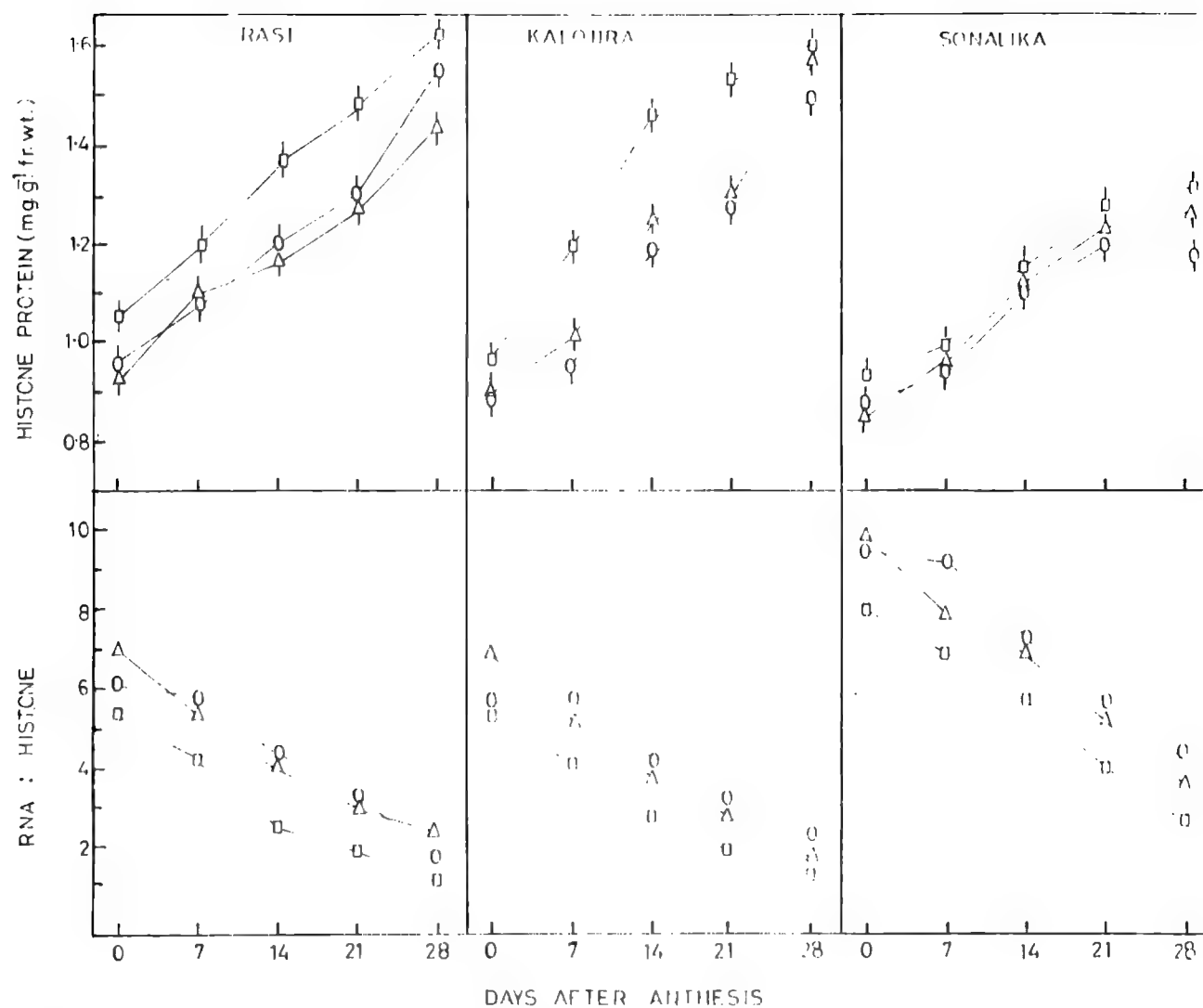
Fig.16. Changes in the content of histone protein and the ratio
of RNA and histone in the flag (O——O), second (△——△)
and third (□——□ ) leaf of two rice and one wheat
cultivars during the progress of reproductive develop-
ment. Data were recorded as in Fig.1. Bars as in Fig.1.
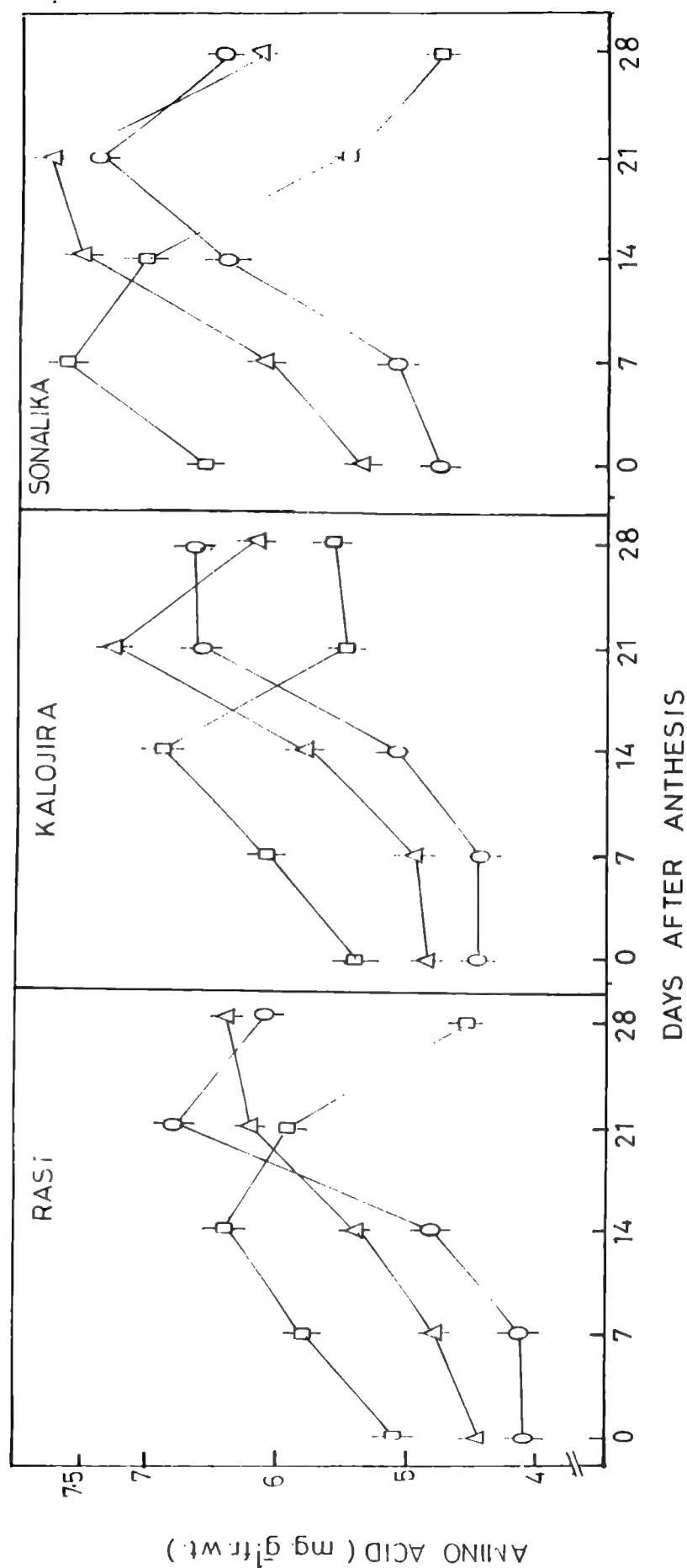
Fig.17. Changes in the accumulation of free amino acids in the flag ( O——O ), second
( △——△ ) and third ( □——□ ) leaf of two rice and one wheat cultivars during
the progress of reproductive development. Data were recorded as in Fig.1.
Bars as in Fig.1.
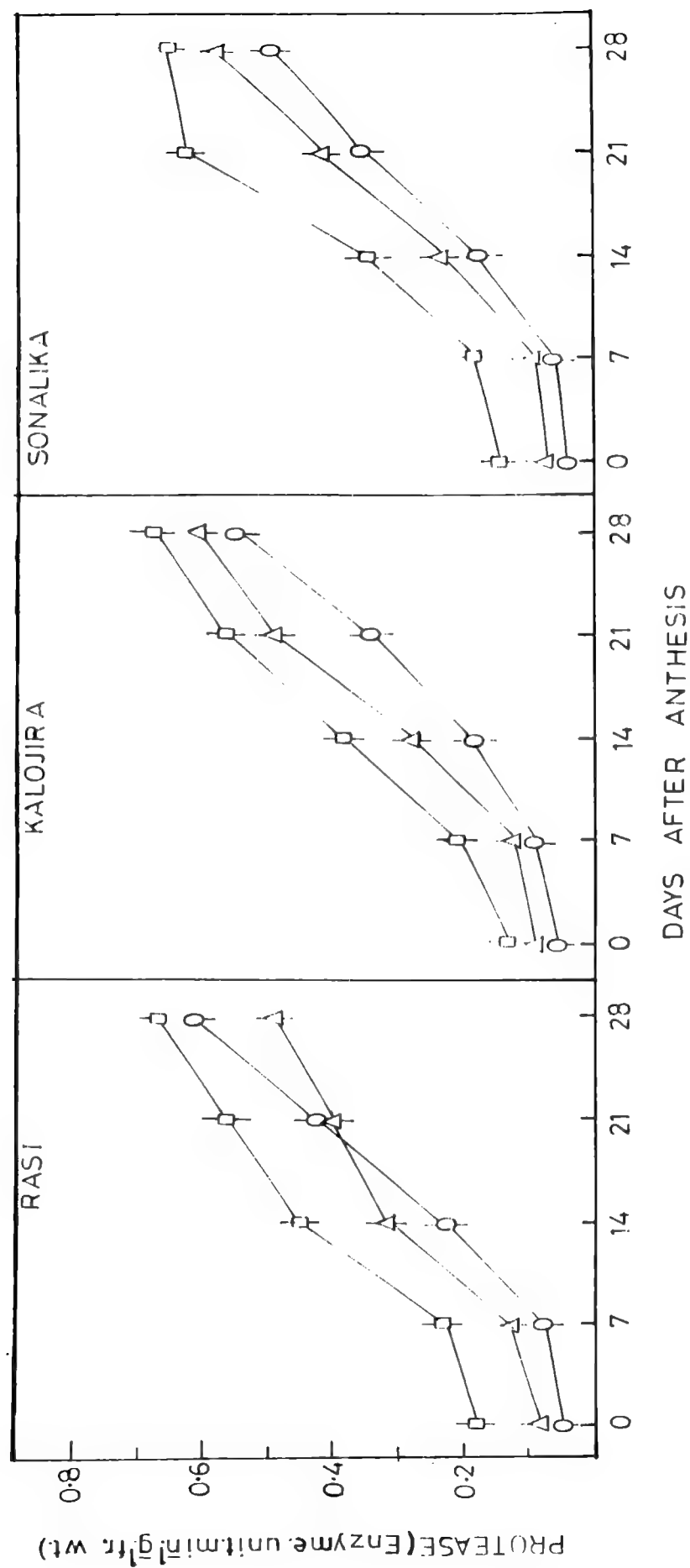
Fig.18. Changes in the protease activity in the flag (O——O), second (△——△) and third (□——□) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

Fig.19. Changes in the content of malondialdehyde and the activity
of superoxide dismutage in the flag (o——o), second (△———△)
and third (□———□) leaf of two rice and one wheat cultivars
during the progress of reproductive development. Data were
recorded as in Fig.1. Bars as in Fig.1.
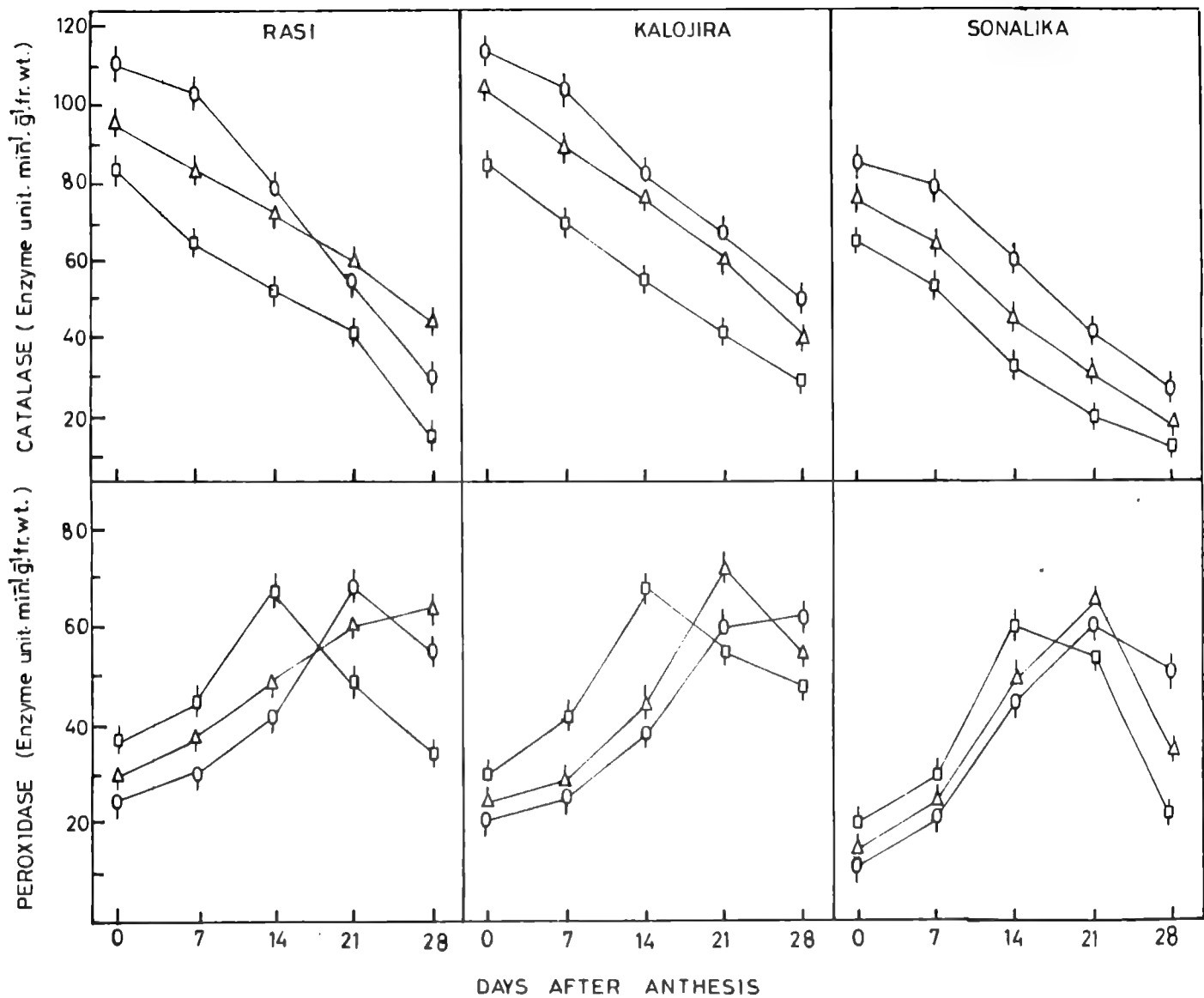
Fig.20. Changes in the activity of catalase and peroxidase in the
flag (o——o ), second (△——△ ) and third ( □——□ ) leaf of
two rice and one wheat cultivars during the progress of
reproductive development. Data were recorded as in Fig.1.
Bars as in Fig.1.
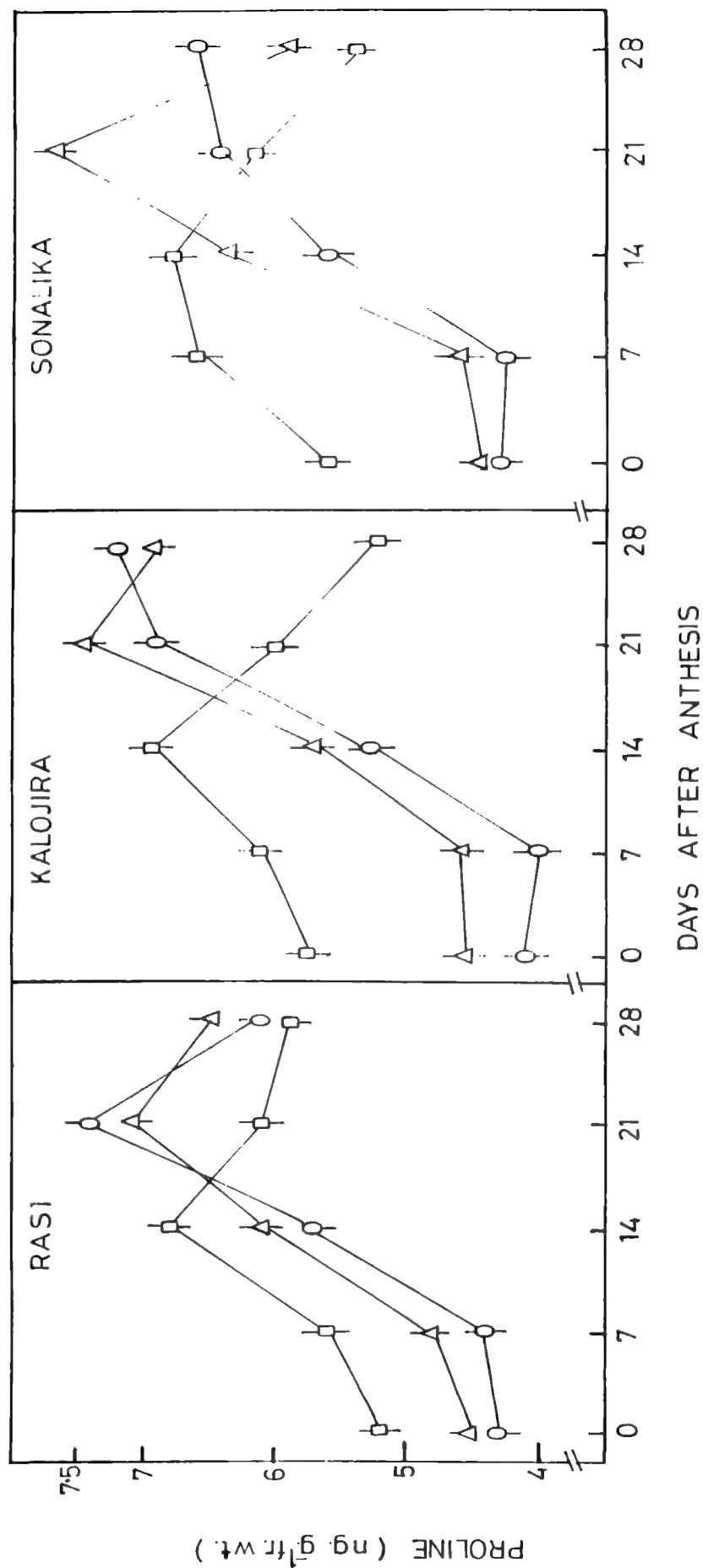
Fig.21. Changes in the accumulation of proline in the flag (O——O), second (△——△) and third (□——□) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

Fig.22. Changes in the content of endogenous cytokinin-like substances in the flag ( ),
second ( ) and third ( ) leaf of two rice and one wheat cultivars
during the progress of reproductive development. Data were recorded as in Fig.1.
Bars as in Fig.1.
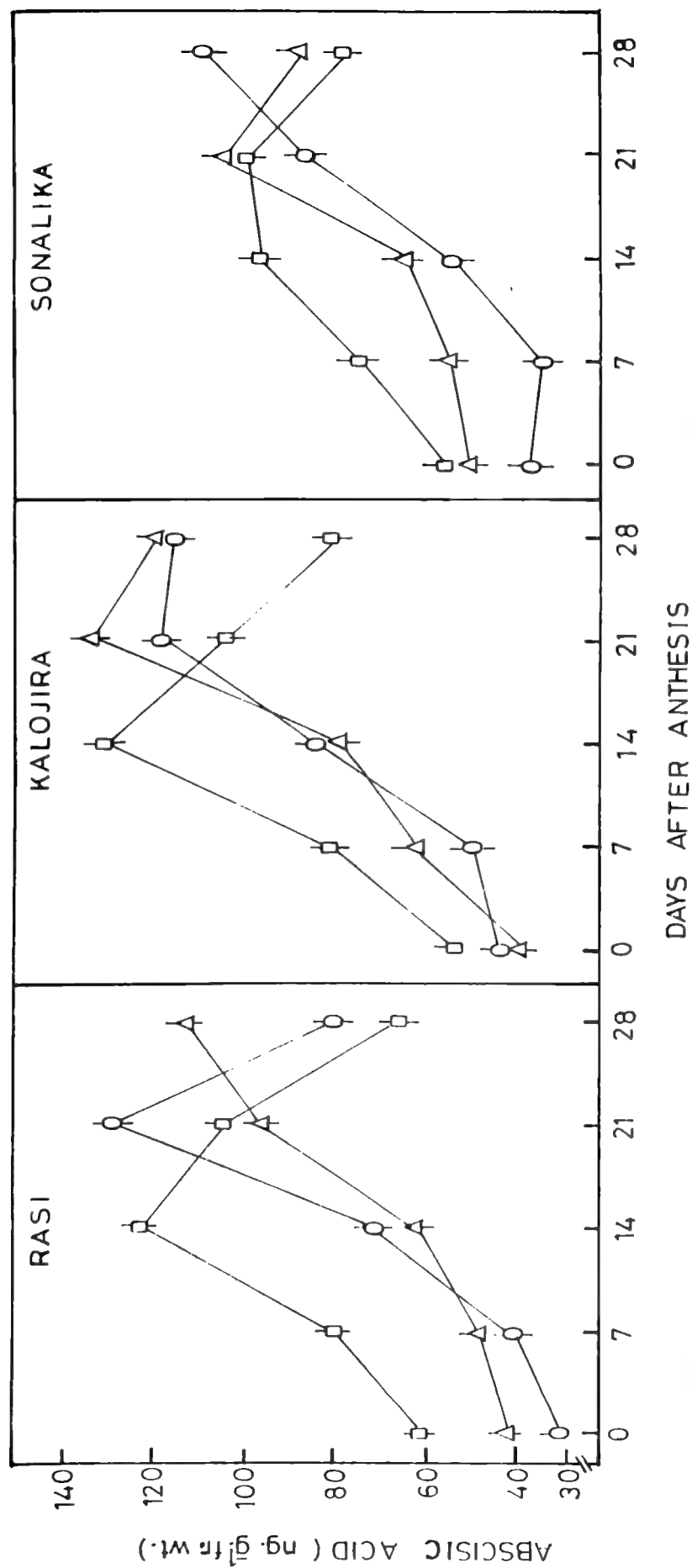
Fig.23. Changes in the content of endogenous abscisic acid in the flag (O——O), second (△——△) and third (□——□) leaf of two rice and one wheat cultivars during the progress of reproductive development. Data were recorded as in Fig.1. Bars as in Fig.1.

Fig.24. Changes in the ratio of cytokinin-like substances to abscisic acid in the flag (○——○), second (△——△) and third (□——□ ) leaf of two rice and one wheat cultivars during the progress of reproductive development.
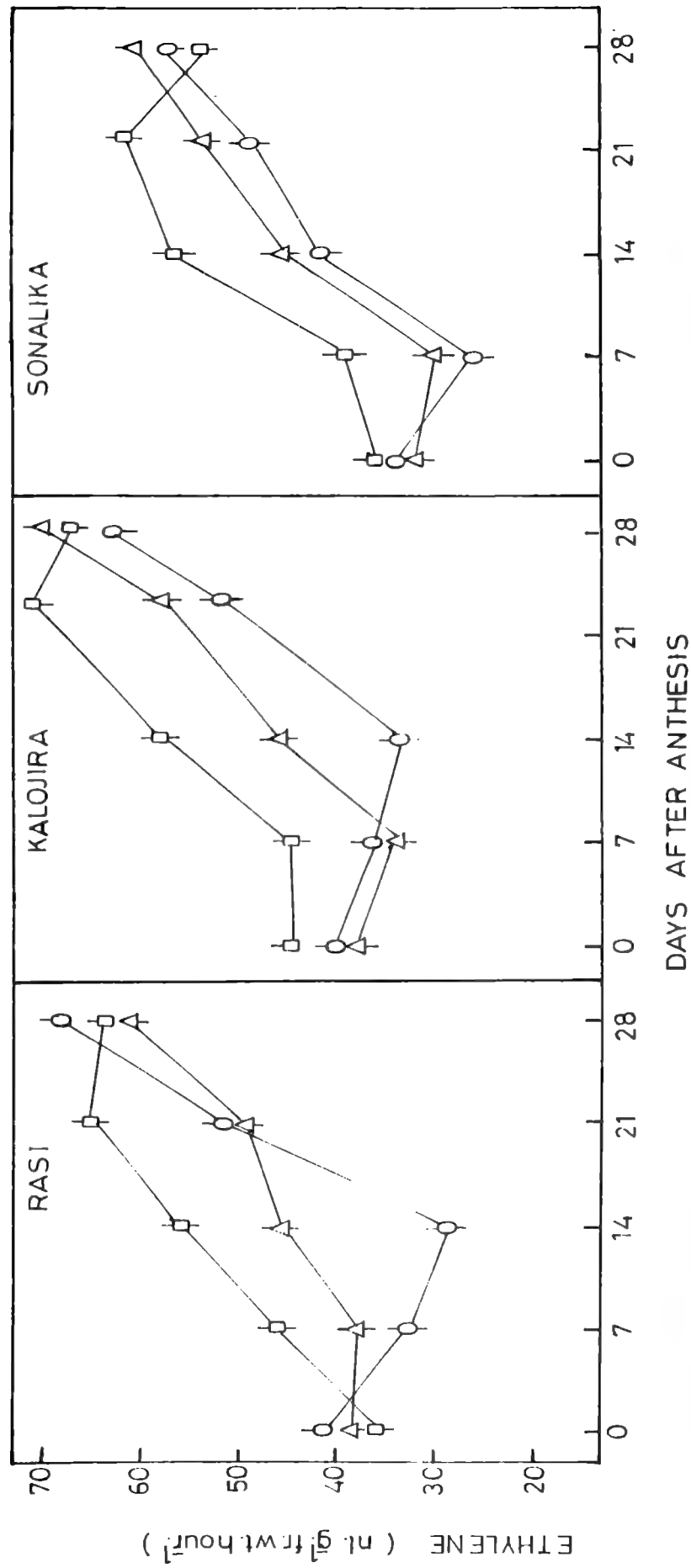
Fig.25. Changes in the evolution of endogenous ethylene from the flag (O——O),
second (Δ——Δ) and third (□——□) leaf of two rice and one wheat cultivars
during the progress of reproductive development.Data were recorded as in
Fig.1. Bars as in Fig.1.
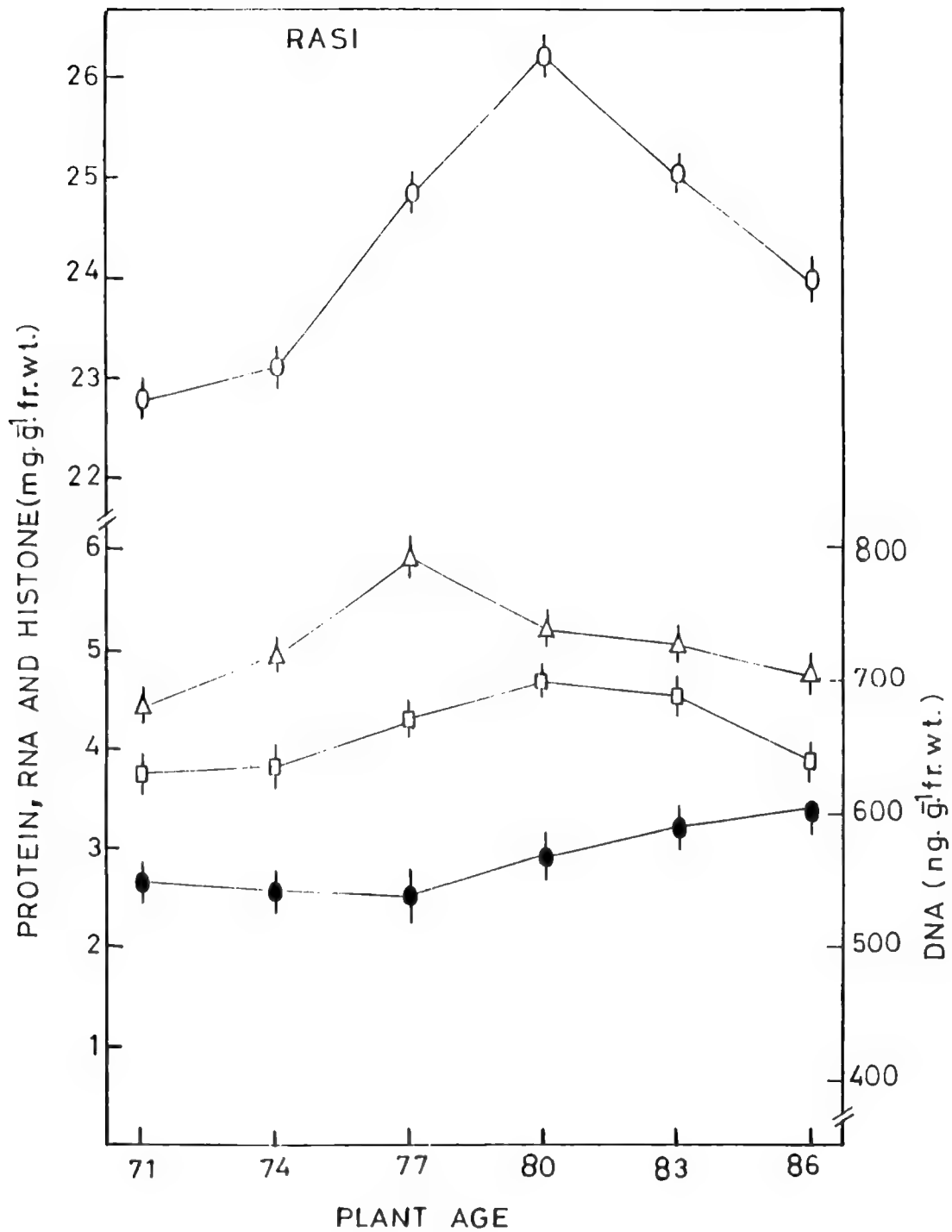
Fig.26. Changes in the content of total protein (○——○),
RNA (△——△), DNA (□——□ ) and histone protein
(●——● ) in the shoot apex of Rasi rice cultivar
prior to panicle emergence. Bars as in Fig.1.
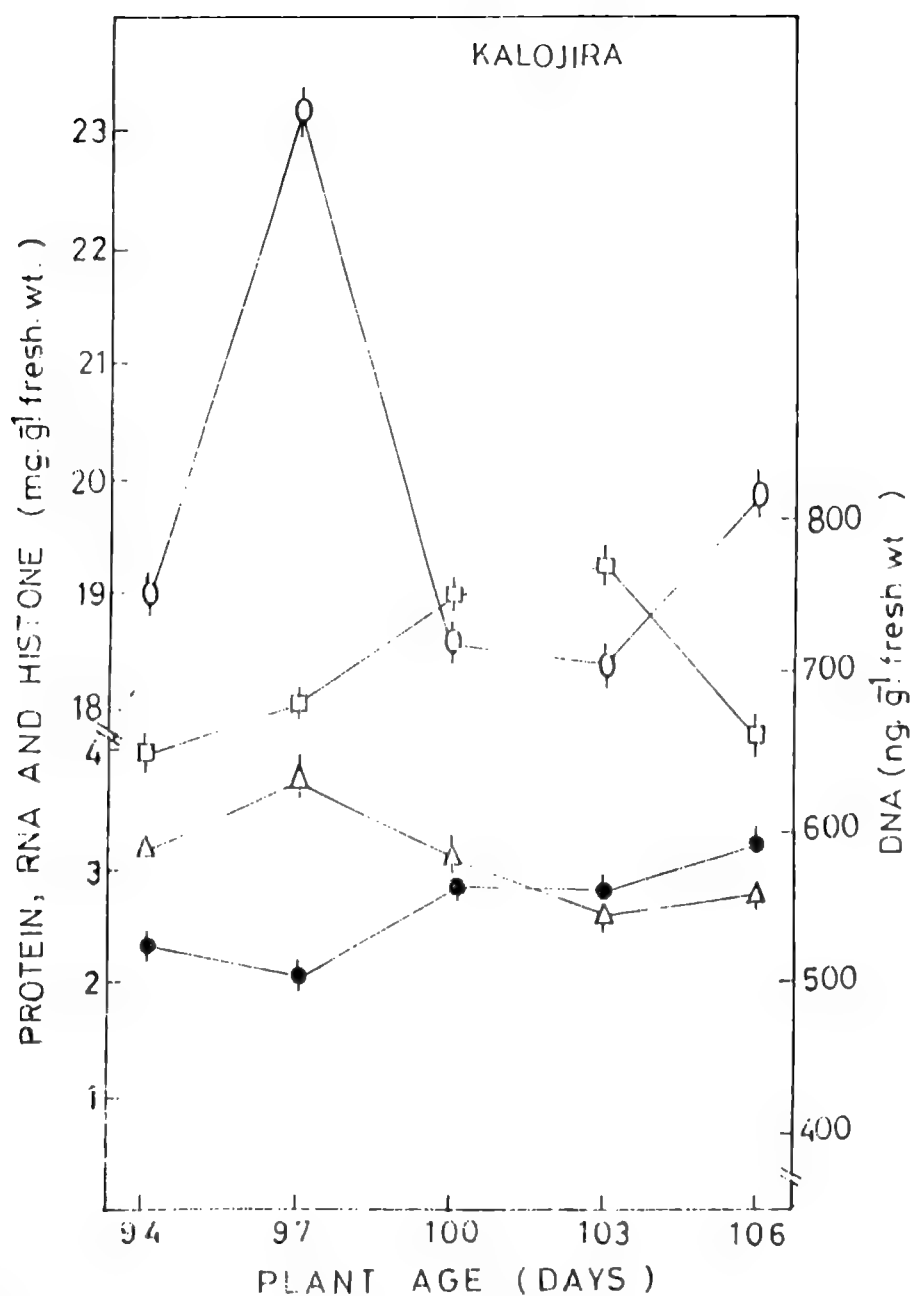
Fig.27. Changes in the content of total protein (O—O) ,
RNA (△—△) , DNA (□—□) and histone protein
(●—●) in the shoot apex of Kalojira rice cul-
tivar prior to panicle emergence. Bars as in Fig.1.
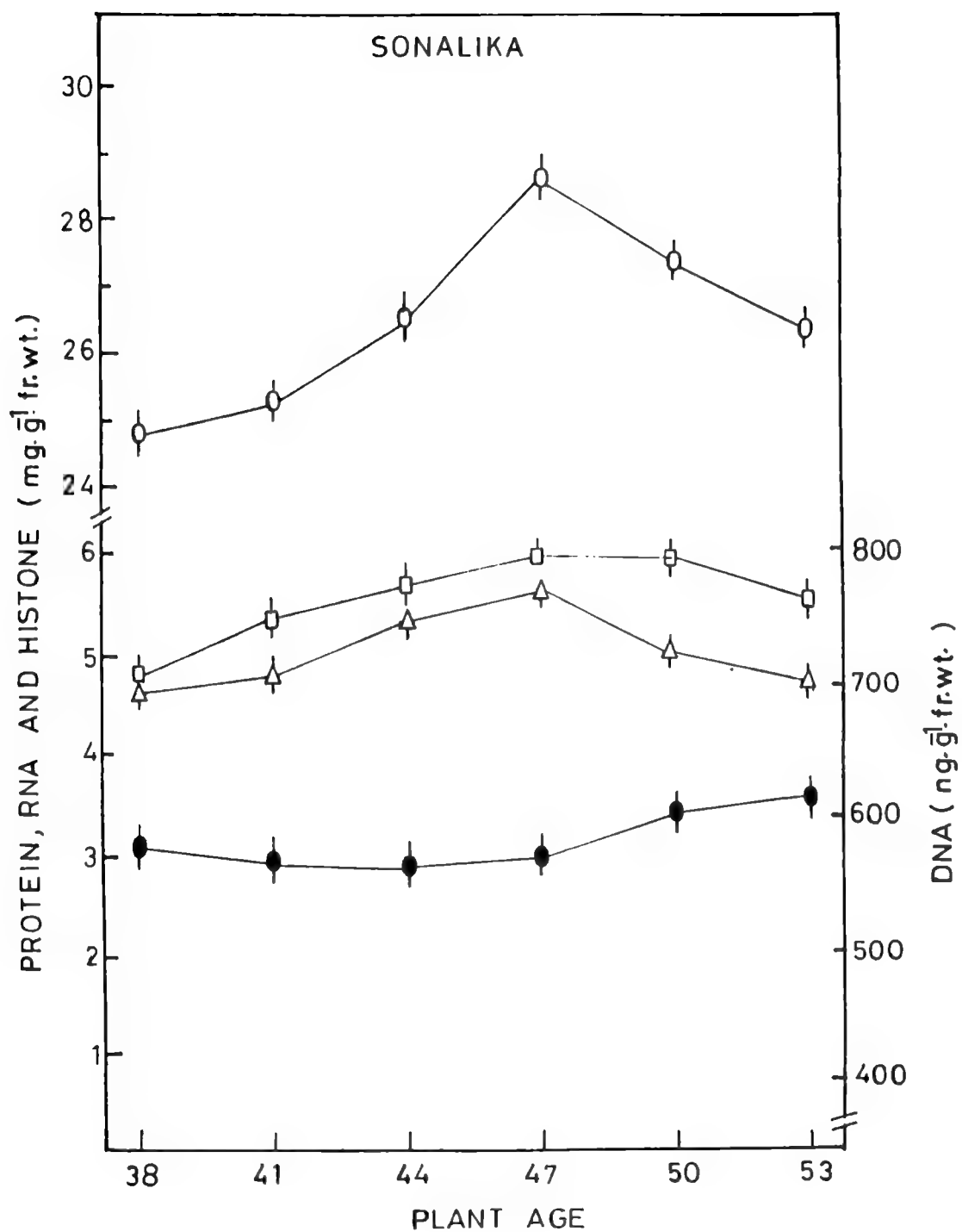
Fig.28. Changes in the content of total protein (o———o),
RNA (△————△), DNA (□————□ ) and histone protein
(●————●) in the shoot apex of Sonalika wheat
cultivar prior to panicle emergence. Bars as in Fig.1.
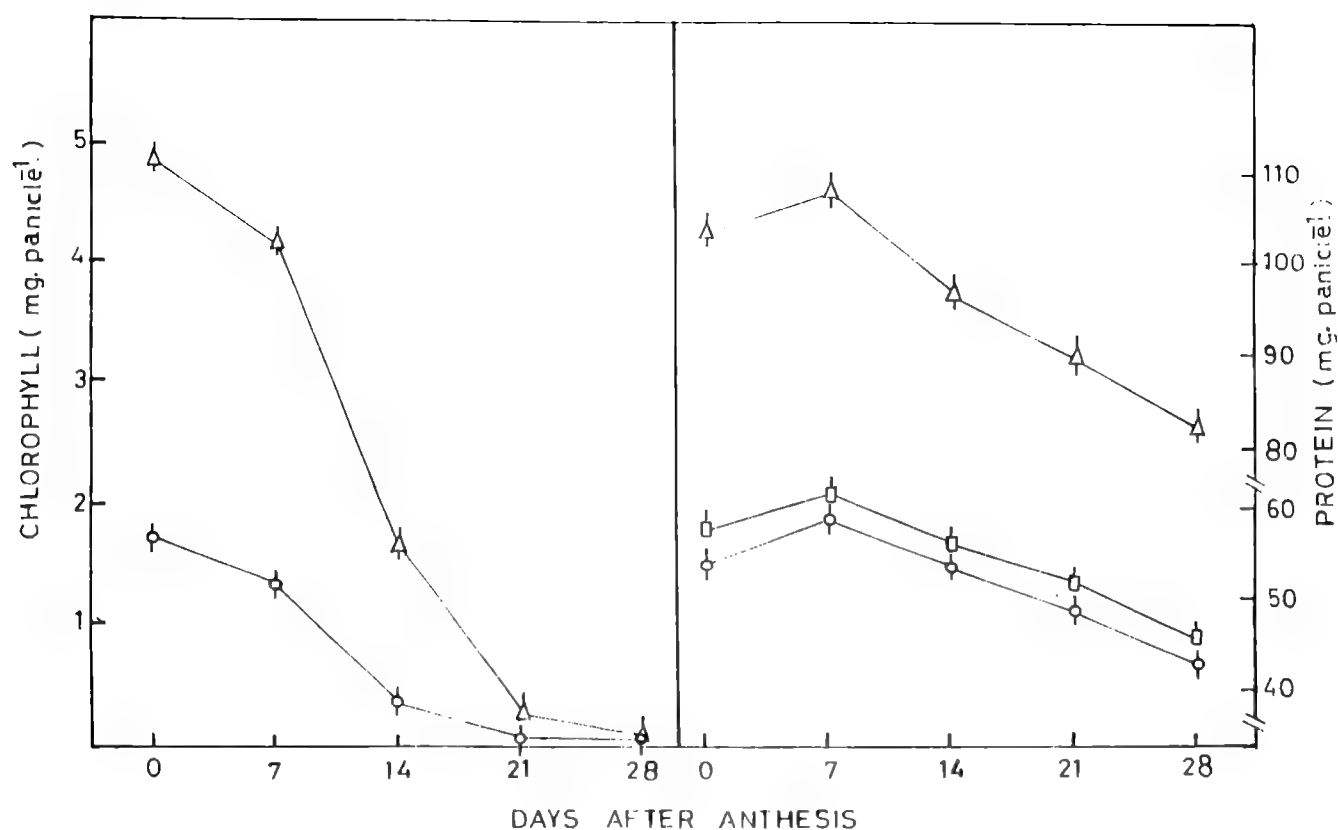
Fig.29. Changes in the content of chlorophyll and protein in
the glumes of rice [Rasi (○——○), Kalojira (□——□)]
and wheat [Sonalika (△——△)] cultivars during the
progress of reproductive development. Data were
recorded as in Fig.1. Bars as in Fig.1.
(N.B: The data of chlorophyll of Kalojira rice cultivar
are not given here due to its very small amount.)

# ★ TABLES ★

Table 1. Total panicle weight and leaf area of different rice and wheat cultivars

| Species | Cultivar | Total panicle weight (g) | Total leaf area ($cm^2$) | | |
|---|---|---|---|---|---|
| | | | Flag | Second | Third |
| Rice | Rasi | 1.920 | 26 | 40 | 36 |
| | Sashyasri | 1.840 | 28 | 42 | 37 |
| | Kalojira | 2.450 | 32 | 33 | 29 |
| | Badsabhog | 2.150 | 34 | 36 | 32 |
| | Patnai | 3.500 | 64 | 70 | 63 |
| | Kalma | 4.200 | 60 | 67 | 61 |
| Wheat | Sonalika | 2.150 | 20 | 25 | 23 |
| | Kalyansona | 2.000 | 18 | 22 | 24 |
| LSD at P = 0.05 | | 0.449 | 1.49 | 2.30 | 2.94 |

Table 2. Plant height, mode of senescence, number of vascular bundles, area of xylem vessels of a bundle and area of the lumen of the largest xylem vessel in rice and wheat cultivars

| Species | Cultivar | Plant height (cm) | Mode of senescence | Number of vascular bundles/t.s. | | Area of xylem vessels in a bundle ($\mu m^2$) | | Area of the largest vessel ($\mu m^2$) | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Flag leaf | Second leaf | Flag leaf | Second leaf | Flag leaf | Second leaf |
| Rice | Rasi | (79-82) | Non-sequential | 15 | 21 | 118.3 | 133.6 | 50.1 | 63.4 |
| | Kalojira | (101-103) | Sequential | 20 | 22 | 75.0 | 81.0 | 42.9 | 45.6 |
| | Patnai | (118-121) | Intermediate | 21 | 25 | 171.0 | 182.0 | 84.9 | 99.6 |
| Wheat | Sonalika | (75-80) | Sequential | 21 | 20 | 56.0 | 63.0 | 28.0 | 31.0 |
| LSD at P = 0.05 | | | – | 2.8 | 2.2 | 3.8 | 5.3 | 2.9 | 4.2 |

Table 3. Effect of benzyladenine on chlorophyll (Chl) and protein (Prot) contents ($mg.g^{-1}$ F.W) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development

| Species | Cultivar | Treatment | Leaf position | Days after anthesis | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | | | 7 | | 14 | | 21 | | 28 | |
| | | | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| Rice | Rasi | Control | Flag | 1.21 | 83.4 | 0.77 | 68.6 | 0.56 | 60.6 | 0.20 | 43.4 |
| | | | Second | 1.18 | 78.1 | 0.72 | 65.5 | 0.54 | 58.3 | 0.29 | 48.0 |
| | | | Third | 0.82 | 64.2 | 0.60 | 56.3 | 0.25 | 49.5 | 0.05 | 41.0 |
| | | BA | Flag | 1.22 | 82.2 | 0.89 | 71.0 | 0.64 | 65.0 | 0.34 | 50.0 |
| | | | Second | 1.20 | 78.9 | 0.84 | 69.0 | 0.58 | 60.0 | 0.38 | 53.3 |
| | | | Third | 0.82 | 64.5 | 0.72 | 58.8 | 0.33 | 53.2 | 0.09 | 45.7 |
| | | LSD at P = 0.05 | | 0.006 | 2.64 | 0.006 | 1.69 | 0.008 | 2.82 | 0.0084 | 2.80 |
| | Kalojira | Control | Flag | 1.16 | 82.0 | 0.76 | 69.6 | 0.52 | 59.0 | 0.31 | 46.0 |
| | | | Second | 0.89 | 74.0 | 0.70 | 63.0 | 0.48 | 54.0 | 0.21 | 43.3 |
| | | | Third | 0.73 | 54.0 | 0.54 | 56.0 | 0.23 | 49.0 | 0.08 | 39.5 |
| | | BA | Flag | 1.09 | 82.8 | 0.81 | 70.9 | 0.56 | 63.0 | 0.37 | 53.0 |
| | | | Second | 0.91 | 74.5 | 0.75 | 66.0 | 0.53 | 58.5 | 0.31 | 48.5 |
| | | | Third | 0.74 | 66.5 | 0.57 | 60.0 | 0.29 | 54.0 | 0.12 | 44.0 |
| | | LSD at P = 0.05 | | 0.004 | 1.96 | 0.001 | 2.0 | 0.03 | 2.68 | 0.06 | 1.84 |
| Wheat | Sonalika | Control | Flag | 1.10 | 65.5 | 0.70 | 59.0 | 0.58 | 48.5 | 0.21 | 38.0 |
| | | | Second | 0.92 | 62.2 | 0.69 | 54.5 | 0.49 | 45.0 | 0.12 | 34.0 |
| | | | Third | 0.79 | 57.2 | 0.53 | 48.0 | 0.32 | 38.8 | 0.04 | 31.0 |
| | | BA | Flag | 1.14 | 71.0 | 0.84 | 62.5 | 0.64 | 56.0 | 0.31 | 44.4 |
| | | | Second | 0.99 | 66.0 | 0.71 | 58.0 | 0.55 | 53.5 | 0.26 | 42.0 |
| | | | Third | 0.75 | 58.5 | 0.56 | 54.0 | 0.36 | 46.0 | 0.06 | 37.5 |
| | | LSD at P = 0.05 | | 0.0085 | 1.33 | 0.09 | 1.08 | 0.01 | 2.9 | 0.009 | 1.88 |

Table 4. Effect of gibberellic acid on chlorophyll (Chl) and protein (Prot) contents (mg.g$^{-1}$ F.M.) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development

| Species | Cultivar | Treatment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 7 | | 14 | | 21 | | 28 | |
| | | | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| Rice | Rasi | Control | Flag | 1.21 | 83.4 | 0.77 | 68.6 | 0.56 | 60.6 | 0.20 | 43.4 |
| | | | Second | 1.18 | 78.1 | 0.72 | 65.5 | 0.54 | 58.3 | 0.29 | 48.0 |
| | | | Third | 0.82 | 64.2 | 0.60 | 56.3 | 0.25 | 45.1 | 0.05 | 41.0 |
| | | GA$_3$ | Flag | 1.22 | 82.2 | 0.86 | 70.0 | 0.59 | 63.7 | 0.29 | 46.6 |
| | | | Second | 1.16 | 79.6 | 0.80 | 66.6 | 0.55 | 60.8 | 0.32 | 49.8 |
| | | | Third | 0.81 | 64.0 | 0.64 | 57.3 | 0.31 | 51.8 | 0.06 | 43.5 |
| | | LSD at P = 0.05 | | 0.002 | 0.58 | 0.02 | 0.84 | 0.008 | 2.84 | 0.004 | 1.65 |
| | Kalojira | Control | Flag | 1.10 | 82.0 | 0.76 | 68.0 | 0.52 | 59.0 | 0.29 | 46.0 |
| | | | Second | 0.89 | 74.5 | 0.70 | 63.0 | 0.48 | 58.0 | 0.21 | 43.0 |
| | | | Third | 0.73 | 64.0 | 0.54 | 56.0 | 0.23 | 49.4 | 0.08 | 39.5 |
| | | GA$_3$ | Flag | 1.08 | 83.1 | 0.78 | 69.3 | 0.56 | 61.0 | 0.33 | 48.1 |
| | | | Second | 0.91 | 75.8 | 0.72 | 64.2 | 0.52 | 59.0 | 0.28 | 46.2 |
| | | | Third | 0.76 | 65.6 | 0.55 | 57.7 | 0.32 | 51.5 | 0.10 | 41.7 |
| | | LSD at P = 0.05 | | 0.012 | 0.46 | 0.009 | 1.2 | 0.006 | 1.62 | 0.03 | 1.02 |
| Wheat | Sonalika | Control | Flag | 1.10 | 65.5 | 0.70 | 59.0 | 0.58 | 48.5 | 0.21 | 38.0 |
| | | | Second | 0.92 | 62.2 | 0.69 | 54.0 | 0.49 | 45.0 | 0.12 | 34.0 |
| | | | Third | 0.79 | 57.2 | 0.52 | 48.0 | 0.32 | 38.8 | 0.04 | 31.0 |
| | | GA$_3$ | Flag | 1.08 | 66.0 | 0.75 | 61.0 | 0.62 | 52.6 | 0.25 | 42.6 |
| | | | Second | 0.93 | 63.0 | 0.69 | 55.3 | 0.51 | 50.0 | 0.18 | 39.5 |
| | | | Third | 0.78 | 57.9 | 0.54 | 51.5 | 0.36 | 41.6 | 0.05 | 33.6 |
| | | LSD at P = 0.05 | | 0.004 | 0.48 | 0.04 | 0.64 | 0.012 | 1.06 | 0.006 | 1.2 |

Table 5. Effect of abscisic acid on chlorophyll (Chl) and protein (Prot) contents ($mg.g^{-1}$ F.W) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development

| Species | Cultivar | Treatment | Leaf position | Days after anthesis | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | | | 7 | | 14 | | 21 | | 28 | |
| | | | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| Rice | Rasi | Control | Flag | 1.21 | 83.4 | 0.77 | 68.6 | 0.56 | 60.6 | 0.20 | 43.4 |
| | | | Second | 1.18 | 78.1 | 0.72 | 65.5 | 0.54 | 58.3 | 0.29 | 48.0 |
| | | | Third | 0.82 | 64.2 | 0.60 | 56.3 | 0.25 | 49.1 | 0.05 | 41.0 |
| | | ABA | Flag | 1.20 | 83.0 | 0.73 | 66.7 | 0.52 | 57.2 | 0.16 | 40.2 |
| | | | Second | 1.13 | 77.0 | 0.70 | 64.0 | 0.50 | 55.5 | 0.22 | 44.3 |
| | | | Third | 0.80 | 63.5 | 0.56 | 54.0 | 0.21 | 46.0 | 0.04 | 36.6 |
| | | LSD at P = 0.05 | | 0.001 | 0.06 | 0.005 | 1.54 | 0.0046 | 0.34 | 0.002 | 1.32 |
| | Kalojira | Control | Flag | 1.10 | 82.0 | 0.76 | 68.0 | 0.52 | 59.0 | 0.29 | 46.0 |
| | | | Second | 0.89 | 74.5 | 0.70 | 63.0 | 0.48 | 54.0 | 0.21 | 43.3 |
| | | | Third | 0.73 | 64.0 | 0.54 | 56.0 | 0.23 | 49.0 | 0.08 | 39.5 |
| | | ABA | Flag | 1.09 | 80.8 | 0.73 | 65.5 | 0.46 | 54.2 | 0.21 | 42.5 |
| | | | Second | 0.89 | 72.2 | 0.61 | 61.8 | 0.42 | 51.5 | 0.16 | 40.5 |
| | | | Third | 0.70 | 63.1 | 0.50 | 53.3 | 0.20 | 46.6 | 0.05 | 36.0 |
| | | LSD at P = 0.05 | | 0.0025 | 0.62 | 0.004 | 1.25 | 0.0062 | 0.66 | 0.002 | 1.82 |
| Wheat | Sonalika | Control | Flag | 1.10 | 65.5 | 0.70 | 59.0 | 0.58 | 48.5 | 0.21 | 38.0 |
| | | | Second | 0.92 | 62.2 | 0.69 | 54.0 | 0.49 | 45.0 | 0.12 | 34.0 |
| | | | Third | 0.79 | 57.2 | 0.52 | 48.0 | 0.32 | 38.8 | 0.04 | 31.0 |
| | | ABA | Flag | 1.06 | 64.5 | 0.67 | 57.2 | 0.53 | 45.5 | 0.14 | 35.5 |
| | | | Second | 0.90 | 62.0 | 0.66 | 53.0 | 0.44 | 43.2 | 0.11 | 32.0 |
| | | | Third | 0.76 | 55.5 | 0.50 | 45.0 | 0.26 | 35.2 | 0.03 | 28.0 |
| | | LSD at P = 0.05 | | 0.0014 | 0.35 | 0.0065 | 0.69 | 0.022 | 1.49 | 0.002 | 0.68 |

Table 6. Effect of (BA + GA$_3$) on chlorophyll (Chl) and protein (Prot) contents (mg.g$^{-1}$ F.W) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development

| Species | Cultivar | Treatment | Leaf position | Days after anthesis | | | | | | | |
| | | | | 7 | | 14 | | 21 | | 28 | |
| | | | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| Rice | Rasi | Control | Flag | 1.21 | 83.4 | 0.77 | 68.6 | 0.56 | 60.6 | 0.20 | 43.4 |
| | | | Second | 1.18 | 78.1 | 0.72 | 65.5 | 0.54 | 58.3 | 0.29 | 48.0 |
| | | | Third | 0.82 | 64.2 | 0.60 | 56.3 | 0.25 | 49.1 | 0.05 | 41.0 |
| | | BA + GA$_3$ | Flag | 1.25 | 84.2 | 0.91 | 74.2 | 0.66 | 65.5 | 0.37 | 51.8 |
| | | | Second | 1.19 | 79.5 | 0.82 | 69.0 | 0.61 | 64.0 | 0.40 | 54.1 |
| | | | Third | 0.82 | 65.5 | 0.61 | 59.6 | 0.33 | 55.4 | 0.07 | 44.4 |
| | | LSD at P = 0.05 | | 0.012 | 0C.49 | 0.003 | 2.10 | 0.009 | 2.10 | 0.0074 | 1.62 |
| | Kalojira | Control | Flag | 1.10 | 82.0 | 0.76 | 68.0 | 0.52 | 59.0 | 0.29 | 46.0 |
| | | | Second | 0.89 | 74.5 | 0.70 | 63.0 | 0.48 | 54.0 | 0.21 | 43.3 |
| | | | Third | 0.73 | 64.0 | 0.54 | 56.0 | 0.23 | 49.0 | 0.08 | 39.5 |
| | | BA + GA$_3$ | Flag | 1.10 | 83.0 | 0.84 | 72.2 | 0.58 | 64.5 | 0.39 | 54.8 |
| | | | Second | 0.87 | 75.5 | 0.76 | 67.0 | 0.53 | 59.0 | 0.33 | 50.3 |
| | | | Third | 0.73 | 65.9 | 0.56 | 61.5 | 0.30 | 56.0 | 0.11 | 44.5 |
| | | LSD at P = 0.05 | | 0.001 | 0.54 | 0.0063 | 0.95 | 0.0069 | 1.94 | 0.009 | 0.56 |
| Wheat | Sonalika | Control | Flag | 1.10 | 65.5 | 0.70 | 59.0 | 0.58 | 48.5 | 0.21 | 38.0 |
| | | | Second | 0.92 | 62.2 | 0.69 | 54.0 | 0.49 | 45.0 | 0.12 | 34.0 |
| | | | Third | 0.79 | 57.2 | 0.52 | 48.0 | 0.32 | 38.8 | 0.04 | 31.0 |
| | | BA + GA$_3$ | Flag | 1.12 | 69.5 | 0.81 | 63.4 | 0.63 | 59.0 | 0.32 | 48.5 |
| | | | Second | 0.94 | 64.2 | 0.74 | 59.5 | 0.56 | 56.3 | 0.29 | 45.5 |
| | | | Third | 0.80 | 57.0 | 0.58 | 55.0 | 0.36 | 47.3 | 0.07 | 38.0 |
| | | LSD at P = 0.05 | | 0.004 | 0.49 | 0.0067 | 1.72 | 0.013 | 1.16 | 0.0073 | 2.80 |

Table 7. Effect of benzyladenine on nitrogen (N) and phosphorus (P) contents in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs. 8 & 9.

| Species | Cultivar | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 7 | | 14 | | 21 | | 28 | |
| | | | N | P | N | P | N | P | N | P |
| Rice | Rasi | Flag | +1.25 | +2.7 | +1.8 | +6.4 | +8.2 | +16.0 | +15.2 | +37.0 |
| | | Second | +0.96 | +1.8 | +1.6 | +6.6 | +15.2 | +12.0 | +10.0 | +23.9 |
| | | Third | +2.0 | +2.0 | +5.6 | +8.3 | +9.1 | +20.0 | +15.5 | +34.0 |
| | Kalojira | Flag | +0.70 | +0.83 | +3.6 | +5.1 | +4.6 | +7.6 | +9.2 | +16.0 |
| | | Second | +0.60 | +1.0 | +4.4 | +5.0 | +8.2 | +18.1 | +12.3 | +18.8 |
| | | Third | +0.70 | +2.7 | +6.4 | +7.5 | +10.2 | +11.0 | +13.0 | +17.5 |
| Wheat | Sonalika | Flag | +1.20 | +1.8 | +4.6 | +8.1 | +5.2 | +12.5 | +18.5 | +24.0 |
| | | Second | +2.60 | +1.6 | +4.8 | +10.2 | +10.2 | +11.7 | +19.4 | +30.4 |
| | | Third | +3.10 | +4.8 | +6.2 | +9.6 | +8.4 | +17.3 | +8.4 | +20.0 |
| LSD at P = 0.05 | | | 0.09 | 0.32 | 0.94 | 0.76 | 1.36 | 1.82 | 2.42 | 1.76 |

Table 8. Effect of gibberellic acid on nitrogen (N) and phosphorus (P) contents in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (−) over control. For absolute values of the control, see Figs.8 & 9.

| Species | Cultivar | Leaf position | Days after anthesis | | | | | | | |
| | | | 7 | | 14 | | 21 | | 28 | |
| | | | N | P | N | P | N | P | N | P |
| Rice | Rasi | Flag | +1.2 | +1.6 | +3.2 | +3.3 | +3.2 | +8.0 | +7.2 | +12.2 |
| | | Second | +0.9 | +2.0 | +2.6 | +3.6 | +2.9 | +6.0 | +4.2 | +14.2 |
| | | Third | +1.2 | +0.4 | +2.0 | +2.0 | +0.8 | +7.5 | +4.7 | +13.3 |
| | Kalojira | Flag | +2.1 | +1.2 | +2.4 | +2.4 | +2.4 | +4.6 | +4.5 | + 7.3 |
| | | Second | +0.0 | +0.9 | +2.0 | +2.1 | +2.0 | +4.2 | +6.4 | + 8.6 |
| | | Third | +0.6 | +2.2 | +3.6 | +3.3 | +4.8 | +5.5 | +8.3 | + 6.8 |
| Wheat | Sonalika | Flag | +1.2 | +0.0 | +2.4 | +2.0 | +2.8 | +3.4 | +4.1 | + 3.4 |
| | | Second | +1.9 | +1.8 | +3.2 | +2.4 | +1.8 | +2.8 | +5.2 | + 5.8 |
| | | Third | +2.3 | +0.0 | +1.6 | +2.8 | +6.2 | +6.2 | +3.5 | + 2.8 |
| | LSD at P = 0.05 | | 0.3 | NS | 0.63 | 0.69 | 0.95 | 1.03 | 1.11 | 1.32 |

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Table 9. Effect of abscisic acid on nitrogen (N) and phosphorus (P) contents in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (−) over control. For absolute values of the control see Figs. 8 & 9.

| Species | Cultivar | Leaf position | Days after anthesis | | | | | | | |
| | | | 7 | | 14 | | 21 | | 28 | |
| | | | N | P | N | P | N | P | N | P |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Rice | Rasi | Flag | −1.25 | −1.4 | −3.5 | −8.3 | −5.6 | −8.0 | −11.5 | −15.3 |
| | | Second | −5.0 | −2.4 | −5.0 | −8.2 | −6.9 | −7.2 | − 8.6 | −13.0 |
| | | Third | −6.0 | −3.1 | −0.86 | −6.0 | −3.5 | −10.0 | − 6.1 | −10.4 |
| | Kalojira | Flag | −1.6 | −3.3 | −8.4 | −5.1 | −4.8 | −4.8 | − 9.4 | − 9.2 |
| | | Second | −1.2 | −1.2 | −1.2 | −6.0 | −4.2 | −10.0 | −14.6 | − 6.8 |
| | | Third | −0.6 | −1.6 | −4.6 | −3.7 | −4.5 | −5.5 | − 5.2 | − 6.5 |
| Wheat | Sonalika | Flag | −0.9 | −3.3 | −4.2 | −4.1 | −5.2 | −7.5 | − 7.6 | −11.3 |
| | | Second | −0.42 | −1.2 | −3.2 | −6.2 | −4.6 | −9.2 | −12.0 | − 8.6 |
| | | Third | −1.6 | −2.6 | −3.9 | −4.7 | −12.2 | −6.3 | − 6.4 | − 5.0 |
| LSD at P = 0.05 | | | 0.31 | 0.23 | 0.63 | 1.49 | 0.89 | 1.62 | 1.6 | 2.13 |

Table 1C. Effect of (BA + GA$_3$) on nitrogen (N) and phosphorus (P) contents in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control see Figs. 8 & 9.

| Species | Cultivar | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 7 | | 14 | | 21 | | 28 | |
| | | | N | P | N | P | N | P | N | P |
| Rice | Rasi | Flag | +1.6 | +2.7 | +3.8 | +8.5 | + 9.5 | +19.9 | +20.0 | +44.0 |
| | | Second | +1.8 | +2.0 | +1.6 | +8.3 | +14.2 | +16.0 | +10.0 | +34.0 |
| | | Third | +0.0 | +3.6 | +5.4 | +8.0 | +11.5 | +24.0 | +18.5 | +38.0 |
| | Kalojira | Flag | +2.0 | +1.2 | +5.6 | +6.6 | + 5.4 | + 9.4 | +12.5 | +19.0 |
| | | Second | +1.2 | +1.1 | +5.5 | +7.2 | + 6.1 | +11.2 | +13.3 | +24.0 |
| | | Third | +0.0 | +3.2 | +4.6 | +7.7 | +11.6 | +19.3 | +18.0 | +23.0 |
| Wheat | Sonalika | Flag | +0.0 | +1.9 | +4.6 | +8.7 | + 5.4 | +12.5 | +20.3 | +26.0 |
| | | Second | +2.4 | +2.4 | +6.2 | +9.3 | +11.0 | +17.2 | +22.0 | +39.0 |
| | | Third | +1.1 | +2.3 | +2.4 | +4.7 | +10.5 | +16.6 | +10.5 | +15.0 |
| LSD at P = 0.05 | | | 0.016 | 0.22 | 0.94 | 1.72 | 1.03 | 2.33 | 2.56 | 3.62 |

Table 11. Effect of benzyladenine on $[^{32}P]$-phosphate mobilization (M) from the fed-leaves to the grains and the retention capacity (R) of leaves in rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs.10 & 12.

| Species | Cultivar | Leaf position | Days after anthesis | | | | | | | |
| | | | 7 | | 14 | | 21 | | 28 | |
| | | | M | R | M | R | M | R | M | R |
| Rice | Rasi | Flag | +8.7 | +6.6 | +9.4 | +8.2 | +7.5 | +10.8 | +6.0 | +16.5 |
| | | Second | +6.2 | +2.5 | +6.6 | +4.2 | +11.0 | +8.4 | +5.2 | +13.5 |
| | | Third | +2.4 | +4.0 | +5.0 | +6.5 | +4.0 | +6.5 | +0.9 | +7.7 |
| | Kalojira | Flag | +16.8 | +12.8 | +11.1 | +8.6 | +6.4 | +9.5 | +8.6 | +9.2 |
| | | Second | +8.4 | +2.6 | +8.3 | +14.0 | +5.4 | +14.2 | +14.0 | +12.2 |
| | | Third | +2.3 | +1.1 | +3.2 | +6.8 | +3.2 | +8.2 | +3.0 | +4.6 |
| Wheat | Sonalika | Flag | +12.0 | +3.2 | +15.0 | +9.5 | +12.0 | +7.5 | +9.0 | +8.4 |
| | | Second | +5.4 | +2.6 | +8.3 | +11.5 | +8.0 | +12.8 | +5.4 | +11.7 |
| | | Third | +3.3 | +3.1 | +6.0 | +16.0 | +4.6 | +5.3 | +3.2 | +9.2 |
| | LSD at P = 0.05 | | 1.09 | 0.56 | 1.4 | 0.98 | 1.62 | 1.09 | 0.82 | 1.24 |

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Table 12. Effect of abscisic acid on [32P]-phosphate mobilization (M) from the fed-leaves to the grains and the retention capacity (R) of leaves in rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (−) over control. For absolute values of the control, see Figs. 10 & 12.

| Species | Cultivar | Leaf position | Days after anthesis | | | | | | | |
| | | | 7 | | 14 | | 21 | | 28 | |
| | | | M | R | M | R | M | R | M | R |
| Rice | Rasi | Flag | − 6.86 | − 0.6 | −13.6 | − 2.4 | − 4.9 | − 6.6 | − 6.6 | −15.0 |
| | | Second | − 8.96 | − 0.64 | −12.5 | − 3.3 | − 2.4 | − 5.4 | − 4.6 | −14.4 |
| | | Third | − 4.40 | − 1.4 | − 3.1 | − 4.0 | − 6.0 | − 8.4 | − 6.8 | − 6.2 |
| | Kalojira | Flag | − 8.6 | − 0.7 | −17.5 | −12.2 | − 8.0 | − 6.2 | − 4.3 | −14.6 |
| | | Second | − 4.2 | − 1.1 | −15.3 | − 8.2 | − 6.0 | − 5.4 | − 2.6 | −11.2 |
| | | Third | − 2.8 | − 2.4 | − 3.2 | − 6.5 | − 3.4 | − 3.2 | − 3.5 | − 5.5 |
| Wheat | Sonalika | Flag | −10.5 | − 1.1 | −16.7 | − 4.0 | − 4.6 | − 2.9 | − 7.4 | −11.1 |
| | | Second | − 4.7 | − 0.9 | − 7.6 | − 6.5 | − 6.8 | − 3.6 | − 5.4 | −16.6 |
| | | Third | − 5.7 | − 1.2 | − 2.7 | − 4.2 | − 3.8 | − 4.4 | − 2.1 | − 5.0 |
| LSD at P = 0.05 | | | 0.69 | 0.04 | 2.21 | 0.82 | 1.33 | 0.84 | 0.24 | 0.72 |

Table 13. Effects of hormones (BA and ABA) on RNA (R), histone protein (H) and RNA/histone ratio (R/H) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (−) over control. For absolute values of the control, see Figs. 15 & 16.

| Species | Cultivar | Treatment | Leaf position | Days after anthesis | | | | | | | | | | | |
| | | | | 7 | | | 14 | | | 21 | | | 28 | | |
| | | | | R | H | R/H | R | H | R/H | R | H | R/H | R | H | R/H |
| Rice | Rasi | BA | Flag | +4.6 | −0.91 | +6.2 | +15.6 | −2.5 | +9.6 | +29.6 | −6.8 | +15.5 | +34.6 | −10.2 | +20.2 |
| | | | 2nd | +6.8 | −0.42 | +5.4 | +23.0 | −3.6 | +12.0 | +26.0 | −7.3 | +13.6 | +32.3 | − 6.3 | +22.5 |
| | | | 3rd | +3.8 | −0.82 | +5.0 | +15.0 | −4.8 | +9.0 | +14.7 | −5.2 | + 8.5 | +18.1 | − 4.6 | +18.0 |
| | | ABA | Flag | −3.4 | +0.44 | −4.8 | − 8.1 | +2.1 | −8.4 | − 2.4 | −4.5 | −11.2 | −13.7 | + 5.4 | −24.0 |
| | | | 2nd | −6.2 | +0.36 | −6.2 | −3.8 | +2.7 | −6.2 | −4.6 | +5.4 | −14.4 | −11.7 | + 6.3 | −22.0 |
| | | | 3rd | −1.9 | +0.82 | −3.3 | −7.5 | +2.4 | −7.5 | −11.7 | +7.2 | −12.0 | − 9.0 | + 3.4 | −14.2 |
| | Kalojira | BA | Flag | +2.9 | +0.0 | +6.6 | +5.2 | −1.8 | +7.3 | +12.4 | −4.8 | +16.6 | +15.7 | − 4.0 | +24.0 |
| | | | 2nd | +1.5 | −1.7 | +5.4 | +4.34 | −8.2 | +8.4 | +10.0 | −7.6 | +20.0 | +20.5 | − 4.5 | +18.6 |
| | | | 3rd | +6.2 | −0.8 | +6.3 | +4.8 | −5.4 | +6.4 | +16.1 | −6.4 | +14.8 | +27.2 | − 9.2 | +16.0 |
| | | ABA | Flag | −3.3 | +1.9 | −4.6 | −7.8 | +4.4 | −6.9 | − 8.8 | +2.1 | −15.5 | −10.1 | + 6.0 | −17.0 |
| | | | 2nd | −2.8 | +0.0 | −3.4 | −3.7 | +8.3 | −5.5 | −10.0 | +9.3 | −10.2 | −12.2 | + 9.4 | −15.8 |
| | | | 3rd | −4.1 | +0.6 | −5.8 | −12.1 | +3.7 | −8.2 | − 6.4 | +4.9 | −15.7 | − 9.4 | +11.2 | −13.3 |
| Wheat | Sonalika | BA | Flag | +2.3 | −0.6 | +3.8 | +11.5 | −10.4 | +9.4 | +13.0 | −11.4 | +10.3 | +20.0 | −13.6 | +21.0 |
| | | | 2nd | +3.7 | −2.4 | +5.4 | +15.0 | − 3.6 | +11.3 | +16.0 | − 8.0 | +15.5 | +19.0 | − 9.5 | +18.0 |
| | | | 3rd | +3.0 | −2.1 | +6.2 | +10.3 | − 5.8 | +6.4 | +22.0 | − 4.2 | +14.5 | +15.4 | − 8.2 | +24.4 |
| | | ABA | Flag | −5.0 | +1.8 | −4.6 | − 5.1 | + 4.5 | −8.2 | − 6.8 | + 6.2 | −16.4 | − 9.0 | − 8.0 | −26.0 |
| | | | 2nd | −2.4 | +3.2 | −4.9 | − 4.5 | + 8.5 | −3.4 | − 5.7 | +13.5 | −17.2 | −15.0 | − 6.7 | −18.5 |
| | | | 3rd | −4.6 | +4.5 | −3.3 | − 5.4 | +12.0 | −6.6 | − 9.0 | +10.0 | −12.0 | −13.7 | − 9.6 | −22.0 |
| LSD at P = 0.05 | | | | 0.42 | 0.64 | 1.2 | 1.42 | 0.84 | 0.96 | 1.44 | 0.64 | 1.58 | 2.0 | 0.64 | 1.32 |

Table 14. Effects of hormones (BA and ABA) on free amino acid (AA) accumulation and protease activity (PA) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control see Figs. 17 & 18.

| Species | Cultivar | Treatment | Leaf position | Days after anthesis | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | | | 7 | | 14 | | 21 | | 28 | |
| | | | | AA | PA | AA | PA | AA | PA | AA | PA |
| Rice | Rasi | BA | Flag | -6.0 | -11.0 | -10.0 | - 8.3 | -16.0 | -18.0 | -15.0 | -20.6 |
| | | | Second | -8.6 | - 2.0 | - 4.0 | - 6.6 | - 9.4 | -13.0 | -10.5 | -16.0 |
| | | | Third | -6.6 | - 4.5 | - 7.4 | -17.0 | - 8.4 | -14.0 | -10.7 | -12.0 |
| | | ABA | Flag | +4.7 | + 2.0 | + 6.0 | + 8.2 | + 9.4 | + 9.2 | -14.4 | +11.0 |
| | | | Second | +2.2 | + 3.2 | + 9.8 | + 5.4 | + 5.2 | + 6.5 | -10.0 | + 5.0 |
| | | | Third | +3.3 | + 3.6 | + 8.2 | +13.0 | + 7.5 | + 8.4 | - 6.0 | + 4.5 |
| | Kalojira | BA | Flag | +1.6 | -12.0 | - 5.4 | -18.2 | -13.0 | -13.0 | -13.6 | -20.0 |
| | | | Second | -2.4 | - 6.0 | - 4.8 | -16.0 | -16.0 | -17.0 | -11.5 | -26.0 |
| | | | Third | -6.1 | - 3.5 | - 9.3 | -12.2 | -10.0 | -16.0 | -12.7 | -19.5 |
| | | ABA | Flag | +2.2 | + 6.2 | + 4.6 | + 8.2 | + 4.6 | + 8.2 | - 9.4 | +10.2 |
| | | | Second | +2.4 | + 3.8 | + 5.2 | +10.3 | + 8.4 | +12.6 | -14.5 | +13.3 |
| | | | Third | -2.5 | + 8.3 | + 5.7 | +11.5 | + 5.1 | + 9.4 | - 8.0 | + 6.6 |
| Wheat | Sonalika | BA | Flag | -3.7 | - 8.5 | - 6.6 | -16.0 | -11.5 | - 9.5 | -10.4 | -10.5 |
| | | | Second | -2.0 | - 3.2 | -12.0 | -12.5 | -16.2 | -16.0 | -15.5 | -16.5 |
| | | | Third | -7.5 | - 4.6 | - 9.3 | -16.2 | - 3.2 | -13.0 | -14.0 | -16.0 |
| | | ABA | Flag | +3.2 | + 6.2 | + 5.1 | + 4.6 | + 6.4 | + 8.0 | - 2.9 | +10.2 |
| | | | Second | +4.8 | + 4.2 | + 4.6 | +10.2 | +13.2 | +11.0 | - 4.8 | +14.4 |
| | | | Third | +3.4 | + 7.0 | +11.0 | + 8.5 | + 6.8 | + 7.6 | - 6.6 | + 6.4 |
| | | LSD at P = 0.05 | | NS | 0.42 | 1.06 | 0.82 | 1.32 | 2.22 | 1.04 | 1.44 |

Table 15. Effects of hormones (BA and ABA) on malondialdehyde (MDA) content and superoxide dismutase (SOD) activity in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (−) over control. For absolute values of the control, see Fig. 19.

| Species | Cultivar | Treat-ment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | 7 | | 14 | | 21 | | 28 | |
| | | | | MDA | SOD | MDA | SOD | MDA | SCD | MDA | SOD |
| Rice | Rasi | BA | Flag | -0.8 | +4.8 | -2.4 | +8.6 | -7.22 | +20.2 | -18.5 | +52.0 |
| | | | Second | -0.0 | +6.4 | -2.8 | +11.0 | -6.8 | +16.5 | -15.4 | +44.0 |
| | | | Third | -1.6 | +12.2 | -4.6 | +9.2 | -11.0 | +18.8 | -16.2 | +46.0 |
| | | ABA | Flag | +0.0 | -1.2 | +1.6 | -4.8 | +5.4 | -6.6 | +11.0 | -18.0 |
| | | | Second | +1.2 | -1.6 | +2.2 | -2.4 | +6.2 | -9.3 | +14.4 | -15.3 |
| | | | Third | +3.1 | -4.2 | +4.6 | -5.5 | +8.4 | -14.5 | +9.5 | -23.0 |
| | Kalojira | BA | Flag | -0.9 | +6.2 | -3.1 | +6.8 | -8.6 | +14.4 | -12.3 | +36.0 |
| | | | Second | -1.8 | +5.4 | -2.4 | +12.3 | -9.5 | +16.2 | -18.5 | +54.0 |
| | | | Third | -0.8 | +5.9 | -5.3 | +13.5 | -15.0 | +18.0 | -19.5 | +41.0 |
| | | ABA | Flag | +1.2 | -2.4 | +1.6 | -4.6 | +4.4 | -8.5 | +9.2 | -16.6 |
| | | | Second | +0.6 | -2.0 | +2.2 | -6.2 | +6.2 | -10.2 | +11.0 | -16.0 |
| | | | Third | +3.2 | -3.4 | +3.6 | -5.2 | +5.4 | -13.5 | +8.5 | -19.0 |
| Wheat | Sonalika | BA | Flag | -0.8 | +5.4 | -2.6 | +12.2 | -8.2 | +15.0 | -13.0 | +46.0 |
| | | | Second | -1.2 | +6.6 | -4.2 | +9.0 | -6.4 | +12.0 | -17.5 | +54.0 |
| | | | Third | -1.9 | +8.4 | -6.6 | +10.5 | -10.0 | +15.5 | -14.5 | +49.0 |
| | | ABA | Flag | +0.9 | -2.0 | +1.4 | -6.4 | +5.5 | -8.3 | +9.6 | -16.3 |
| | | | Second | +0.6 | -1.6 | +1.6 | -5.5 | +5.8 | -10.5 | +7.2 | -18.6 |
| | | | Third | +1.2 | -4.6 | +3.4 | -6.6 | +8.9 | -7.5 | +12.5 | -12.2 |
| LSD at P = 0.05 | | | | NS | 0.84 | 1.24 | 1.19 | 1.09 | 1.42 | 1.16 | 2.28 |

Table 16. Effects of hormones (BA and ABA) on the activity of catalase (Cata) and peroxidase (Pero) in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Fig. 20.

| Species | Cultivar | Treatment | Leaf position | Days after anthesis | | | | | | | |
| | | | | 7 | | 14 | | 21 | | 28 | |
| | | | | Cata | Pero | Cata | Pero | Cata | Pero | Cata | Pero |
| Rice | Rasi | BA | Flag | +6.0 | +6.0 | +8.6 | +22.0 | +13.3 | +18.2 | +52.0 | +19.3 |
| | | | Second | +2.3 | +5.5 | +7.0 | +14.0 | +11.2 | +14.5 | +38.0 | +13.6 |
| | | | Third | +10.2 | +3.2 | +13.4 | +8.4 | +24.5 | +15.0 | +28.0 | +12.2 |
| | | ABA | Flag | +2.0 | +4.2 | -7.2 | -9.0 | -10.0 | -12.3 | -16.0 | -8.0 |
| | | | Second | -6.9 | -5.1 | -5.5 | -6.0 | -6.4 | -6.8 | -15.0 | -10.2 |
| | | | Third | -4.6 | -4.0 | -4.3 | -8.2 | -20.0 | -15.0 | -28.0 | -16.0 |
| | Kalojira | BA | Flag | +2.2 | +11.0 | +5.2 | +22.0 | +14.0 | +15.4 | +25.0 | +6.2 |
| | | | Second | +2.4 | +14.0 | +5.5 | +12.0 | +18.0 | +20.0 | +33.0 | +15.0 |
| | | | Third | +4.5 | +8.3 | +7.2 | +16.0 | +16.0 | +14.0 | +50.0 | +10.4 |
| | | ABA | Flag | -2.4 | -4.2 | -4.9 | -5.9 | -8.5 | -4.6 | -13.4 | -7.2 |
| | | | Second | -4.4 | -2.6 | -6.2 | -6.2 | -10.2 | -12.4 | -16.5 | -18.2 |
| | | | Third | -6.2 | -6.2 | -6.5 | -10.0 | -10.5 | -11.5 | -10.0 | -8.5 |
| Wheat | Sonalika | BA | Flag | +2.7 | +6.2 | +10.3 | +12.0 | +22.0 | +16.5 | +45.0 | +26.0 |
| | | | Second | -2.4 | +3.6 | +16.0 | +10.0 | +24.0 | +18.7 | +44.0 | +24.0 |
| | | | Third | +5.3 | +6.6 | +14.0 | +14.0 | +30.0 | +9.6 | +36.0 | +20.0 |
| | | ABA | Flag | -2.0 | -4.2 | -6.6 | -8.4 | -5.5 | -7.6 | -16.0 | -8.0 |
| | | | Second | -0.0 | -3.1 | -6.0 | -12.2 | -10.5 | -10.2 | -12.0 | -15.4 |
| | | | Third | -3.5 | -8.4 | -10.0 | -6.8 | -5.5 | -8.3 | -13.0 | -7.8 |
| LSD at P = 0.05 | | | | 0.62 | NS | 0.46 | 1.84 | 1.62 | 1.24 | 2.06 | 1.48 |

Table 17. Changes in the rate of transpiration (mg.cm$^{-2}$.h$^{-1}$) by the whole plant and the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. The leaves whose transpiration rate not being measured, were smeared with vaseline on both sides.

| Species | Cultivar | Transpiration by | Days after anthesis | | | | |
|---|---|---|---|---|---|---|---|
| | | | 0 | 7 | 14 | 21 | 28 |
| Rice | Rasi | Total plant | 18.2 | 17.8 | 16.0 | 13.6 | 7.4 |
| | | Only flag leaf | 24.5 | 23.9 | 21.0 | 16.4 | 10.8 |
| | | Only second leaf | 23.0 | 23.4 | 20.0 | 15.8 | 12.6 |
| | | Only third leaf | 21.0 | 20.0 | 16.2 | 12.0 | 6.4 |
| | Kalojira | Total plant | 14.0 | 13.4 | 12.8 | 9.6 | 6.8 |
| | | Only flag leaf | 21.2 | 21.0 | 18.4 | 14.5 | 9.9 |
| | | Only second leaf | 20.0 | 20.5 | 18.0 | 14.4 | 8.4 |
| | | Only third leaf | 17.6 | 16.4 | 13.4 | 11.2 | 6.0 |
| Wheat | Sonalika | Total plant | 12.2 | 12.6 | 11.0 | 9.2 | 5.8 |
| | | Only flag leaf | 18.0 | 18.4 | 16.0 | 14.4 | 9.5 |
| | | Only second leaf | 19.6 | 19.0 | 17.3 | 13.7 | 8.6 |
| | | Only third leaf | 17.0 | 15.4 | 12.2 | 8.5 | 5.4 |
| LSD at P = 0.05 | | | 0.74 | 0.58 | 1.46 | 0.42 | 0.59 |

Table 18. Effects of hormones (BA and ABA) on the rate of transpiration by rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Table 17.

| Species | Cultivar | Transpiration by | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | BA | | | | ABA | | | |
| | | | 7 | 14 | 21 | 28 | 7 | 14 | 21 | 28 |
| Rice | Rasi | Total plant | +2.4 | +3.2 | +16.2 | +24.4 | -0.8 | -4.4 | -8.2 | -14.3 |
| | | Flag leaf | +3.4 | +4.6 | +13.3 | +16.0 | -2.1 | -3.3 | -5.8 | -11.2 |
| | | Second leaf | +4.9 | +6.7 | +12.0 | +20.0 | -0.9 | -2.5 | -6.4 | - 9.5 |
| | | Third leaf | +8.4 | +6.8 | +15.0 | + 8.5 | -2.4 | -6.6 | -10.0 | - 8.5 |
| | Kalotira | Total plant | +0.9 | +4.5 | + 8.2 | +21.5 | -0.8 | -4.2 | -8.4 | -10.8 |
| | | Flag leaf | +1.8 | +3.8 | + 9.4 | +22.6 | -0.6 | -3.1 | -7.2 | -13.3 |
| | | Second leaf | +2.4 | +5.4 | + 7.5 | +26.4 | -1.2 | -3.6 | -6.8 | -12.3 |
| | | Third leaf | -3.1 | +6.0 | +10.0 | +10.2 | -1.8 | -5.2 | -10.6 | - 9.5 |
| Wheat | Sonalika | Total plant | +1.6 | +3.6 | +11.4 | +16.0 | -2.2 | -3.6 | -8.5 | -10.6 |
| | | Flag leaf | +0.9 | +6.5 | +12.2 | +18.4 | -0.9 | -1.2 | -5.2 | -12.4 |
| | | Second leaf | +1.9 | +5.2 | + 9.5 | +15.2 | -1.2 | -2.2 | -6.5 | -12.5 |
| | | Third leaf | +3.2 | +6.1 | + 6.4 | + 9.5 | -2.6 | -6.2 | -9.2 | -12.8 |
| | | LSD at P = 0.05 | 0.06 | 0.41 | 0.76 | 1.03 | 0.06 | 0.32 | 0.87 | 0.56 |

Table 10. Effects of hormones (BA and ABA) on proline accumulation in the flag, second and third leaf of rice and wheat cultivars during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Fig. 21.

| Species | Cultivar | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | BA | | | | ABA | | | |
| | | | 7 | 14 | 21 | 28 | 7 | 14 | 21 | 28 |
| Rice | Rasi | Flag | -2.1 | -5.5 | -11.2 | -13.4 | +4.3 | +7.4 | +12.5 | +9.4 |
| | | Second | -4.1 | -10.1 | -7.3 | -8.2 | +2.0 | +6.0 | +8.4 | +8.4 |
| | | Third | +0.0 | -6.9 | -15.0 | -5.8 | +6.4 | +2.7 | +8.9 | +7.8 |
| | Kalotika | Flag | -9.5 | -3.7 | -11.4 | -8.2 | +4.5 | +11.0 | +9.2 | +6.4 |
| | | Second | -3.9 | -11.6 | -9.7 | -12.8 | +1.9 | +6.0 | +10.2 | +9.5 |
| | | Third | -3.5 | -10.1 | -3.2 | -6.8 | +5.7 | +6.7 | +16.4 | +9.6 |
| Wheat | Sonalika | Flag | -4.5 | -5.1 | -9.7 | -10.4 | +2.2 | +8.6 | +6.0 | +13.3 |
| | | Second | -2.1 | -4.4 | -8.0 | -13.6 | +4.2 | +4.4 | +8.4 | -17.4 |
| | | Third | -0.8 | -7.2 | -6.1 | -11.0 | +4.9 | +5.7 | +13.3 | +9.0 |
| LSD at P = 0.05 | | | 0.46 | 0.76 | 1.84 | 0.64 | 0.16 | 0.36 | 0.89 | 1.06 |

Table 20. Effect of panicle removal at different reproductive stages on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g⁻¹.F.W.) in the flag, second and third leaf of rice (cv. Rasi) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control.

| Treatment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| Control | Flag | 1.22 | 71.0 | 0.79 | 60.0 | 0.34 | 49.0 | 0.12 | 37.0 |
| | Second | 0.96 | 62.0 | 0.71 | 56.0 | 0.36 | 46.0 | 0.20 | 44.0 |
| | Third | 0.72 | 58.5 | 0.52 | 50.0 | 0.16 | 40.5 | 0.04 | 33.8 |
| Panicle removed at 0 DAA (anthesis stage) | Flag | 1.16(-4.9) | 72.0(+1.4) | 0.93(+18) | 62.0(+3.3) | 0.43(+26) | 59.2(+16) | 0.27(+125) | 48.5(+31) |
| | Second | 0.98(+2.0) | 63.4(+2.2) | 0.74(-5) | 53.0(-3.4) | 0.46(+27) | 54.5(+17) | 0.26(+30) | 47.0(+6.8) |
| | Third | 0.73(+2.7) | 60.5(+3.4) | 0.54(+3) | 52.2(-4.0) | 0.19(+18) | 44.5(+10) | 0.08(+100) | 38.4(+12.0) |
| Panicle removed at 7 DAA (grain filling stage) | Flag | - | - | 0.78(+1.2) | 60.5(-0.3) | 0.42(+23) | 55.5(+12) | 0.25(+109) | 47.5(+28) |
| | Second | - | - | 0.73(+2.8) | 60.6(+8.2) | 0.44(+22) | 51.0(+12) | 0.24(+20) | 47.0(+6.8) |
| | Third | - | - | 0.53(+2.0) | 52.3(+4.6) | 0.19(+18) | 45.3(-12) | 0.07(+75) | 37.0(+9.4) |
| Panicle removed at 14 DAA (grain development stage) | Flag | - | - | - | - | 0.35(+2.9) | 50.2(+2.0) | 0.13(+8.3) | 38.0(+2.8) |
| | Second | - | - | - | - | 0.36(+0) | 47.2(+2.5) | 0.20(+0) | 41.5(-5.6) |
| | Third | - | - | - | - | 0.15(-6.0) | 40.0(-2.3) | 0.05(+25) | 34.4(+3.8) |
| Panicle removed at 21 DAA (grain maturation stage) | Flag | - | - | - | - | - | - | 0.135(+12.6) | 38.0(+2.6) |
| | Second | - | - | - | - | - | - | 0.190(-8.4) | 45.0(+2.4) |
| | Third | - | - | - | - | - | - | 0.03(-25) | 34.0(+1.6) |
| LSD at P = 0.05 | | 0.0082 | 0.36 | 0.0039 | 1.2 | 0.0046 | 1.54 | 0.0094 | 1.33 |

Table 21. Effect of panicle removal at different reproductive stages on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g$^{-1}$. F.W.) in the flag, second and third leaf of rice plant (cv. Kalojira) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control.

| Treatment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 29 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| Control | Flag | 1.04 | 82.0 | 0.78 | 68.0 | 0.54 | 59.0 | 0.29 | 47.0 |
| | Second | 0.96 | 76.0 | 0.72 | 64.0 | 0.46 | 54.0 | 0.22 | 44.0 |
| | Third | 0.74 | 62.5 | 0.53 | 55.0 | 0.26 | 46.0 | 0.06 | 38.0 |
| Panicle removed at 0 DAA (anthesis stage) | Flag | 1.03(-0.9) | 83.4(+1.7) | 0.81(+3.8) | 71.0(+4.4) | 0.59(+9.2) | 64.0(+8.4) | 0.40(+37) | 53.0(+14) |
| | Second | 0.98(+2.0) | 76.0(+0) | 0.74(+2.7) | 66.0(+3.1) | 0.51(+10) | 58.0(+7.4) | 0.32(+45) | 50.0(+13) |
| | Third | 0.74(+0) | 60.6(-3.6) | 0.56(+5.6) | 56.5(+3.0) | 0.21(-11.5) | 50.4(-9.5) | 0.09(+50) | 42.0(+10.5) |
| Panicle removed at 7 DAA (grain filling stage) | Flag | – | – | 0.77(-1.2) | 69.0(+1.6) | 0.57(-5.5) | 62.4(-5.7) | 0.38(+33) | 51.5(+8.5) |
| | Second | – | – | 0.74(+2.7) | 66.0(+3.1) | 0.52(+13) | 58.5(-7.4) | 0.29(+32) | 49.0(-11) |
| | Third | – | – | 0.56(+5.6) | 57.0(+3.6) | 0.28(+7.6) | 48.8(-6.0) | 0.08(+33) | 41.2(+8) |
| Panicle removed at 14 DAA (grain devet. stage) | Flag | – | – | – | – | 0.53(-1.8) | 58.0(+1.8) | 0.30(+3.4) | 48.5(+3.2) |
| | Second | – | – | – | – | 0.48(+4.3) | 55.2(-1.9) | 0.20(-9) | 44.2(+0.8) |
| | Third | – | – | – | – | 0.27(+4.2) | 45.0(-2.6) | 0.06(+0) | 39.0(+2.6) |
| Panicle removed at 21 DAA (grain maturation stage) | Flag | – | – | – | – | – | – | 0.30(+3.4) | 47.2(+0.8) |
| | Second | – | – | – | – | – | – | 0.20(+9) | 43.0(+2.4) |
| | Third | | | | | | | 0.07(+16) | 39.4(+2.3) |
| LSD at P = 0.05 | | NS | 0.36 | 0.005 | 0.87 | 0.008 | 1.24 | 0.006 | 1.68 |

Table 22. Effect of panicle removal at different reproductive stages on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g$^{-1}$ . F.W.) in the flag, second and third leaf of wheat plant (cv. Sonalika) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control.

| Treatment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| Control | Flag | 1.01 | 68.0 | 0.74 | 56.0 | 0.53 | 48.0 | 0.20 | 39.0 |
| | Second | 0.92 | 61.0 | 0.63 | 51.0 | 0.44 | 43.0 | 0.12 | 34.0 |
| | Third | 0.74 | 54.0 | 0.51 | 47.0 | 0.21 | 49.0 | 0.04 | 30.0 |
| Panicle removed at 0 DAA (anthesis stage) | Flag | 1.09(-8.1) | 72.2(+6.1) | 0.76(+2.7) | 58.0(+3.5) | 0.59(+11.3) | 52.0(+8.4) | 0.26(-30) | 44.0(+12) |
| | Second | 0.93(-1.0) | 63.0(+3.2) | 0.65(+3.1) | 54.0(+5.8) | 0.47(+6.8) | 48.0(+11.6) | 0.19(+36) | 37.8(+11) |
| | Third | 0.76(-2.7) | 54.5(+1.2) | 0.53(+4.0) | 50.0(+6.4) | 0.26(+23) | 41.4(+5.3) | 0.06(+50) | 33.5(+11) |
| Panicle removed at 7 DAA (grain filling stage) | Flag | — | — | 0.73(-1.3) | 57.0(+1.3) | 0.56(+5.6) | 49.5(+2.4) | 0.22(-10) | 41.0(+7.6) |
| | Second | — | — | 0.64(+1.5) | 54.0(+5.8) | 0.43(+2.3) | 44.0(+2.6) | 0.14(+16) | 35.5(+4.4) |
| | Third | — | — | 0.52(+2.0) | 56.5(-1.0) | 0.24(+8.5) | 40.5(+3.6) | 0.046(+15) | 31.6(+5.3) |
| Panicle removed at 14 DAA (grain devet. stage) | Flag | — | — | — | — | 0.53(+0) | 49.0(+2.2) | 0.21(+5) | 40.0(+2.5) |
| | Second | — | — | — | — | 0.45(+2.3) | 42.6(-1.6) | 0.11(+8) | 33.6(-1.6) |
| | Third | — | — | — | — | 0.23(+8.6) | 38.5(-1.8) | 0.05(+25) | 31.0(+3.1) |
| Panicle removed at 21 DAA (grain maturation stage) | Flag | — | — | — | — | — | — | 0.20(+0) | 40.0(+2.6) |
| | Second | — | — | — | — | — | — | 0.13(+8) | 33.0(-3.4) |
| | Third | — | — | — | — | — | — | 0.04(+0) | 30.5(+1.6) |
| LSD at P = 0.05 | | 0.0033 | 0.62 | 0.0041 | 0.94 | 0.0068 | 1.20 | 0.0051 | 1.06 |

Table 23. Effect of panicle removal at different reproductive stages on changes in nitrogen and phosphorus contents (mg.g$^{-1}$.D.W.) in the flag, second and third leaf of rice plant (cv. Rasi) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control

| Treatment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | Nitrogen | Phosphorus | Nitrogen | Phosphorus | Nitrogen | Phosphorus | Nitrogen | Phosphorus |
| Control | Flag | 30.8 | 7.2 | 28.0 | 6.5 | 25.2 | 5.2 | 18.5 | 3.4 |
| | Second | 32.3 | 7.4 | 29.2 | 6.1 | 26.0 | 5.8 | 20.2 | 4.4 |
| | Third | 25.1 | 6.3 | 22.5 | 5.6 | 21.6 | 3.6 | 16.4 | 2.5 |
| Panicle removed at 0 DAA (anthesis stage) | Flag | 32.7(+6.0) | 7.4(+2.7) | 29.1(+4.0) | 7.2(+10.7) | 28.0(+12.8) | 6.08(+17) | 24.6(+30.6) | 5.2(+52) |
| | Second | 33.0(+2.7) | 7.4(+0) | 30.5(+4.1) | 6.7(+9.8) | 28.4(+9.2) | 6.49(18.4) | 24.0(+20) | 5.0(+13) |
| | Third | 25.5(+1.9) | 6.5(+3.1) | 24.2(+7.7) | 5.4(-3.5) | 24.3(+14.7) | 3.68(-2.2) | 18.2(+13) | 3.15(+26) |
| Panicle removed at 7 DAA (grain filling stage) | Flag | - | - | 28.7(+2.5) | 6.7(+3.0) | 27.0(-7.2) | 6.13(-18) | 23.6(+26) | 4.3(+44) |
| | Second | - | - | 30.3(-3.7) | 6.2(-1.3) | 29.4(-11.9) | 6.22(-7.2) | 23.0(+15) | 5.0(-22) |
| | Third | | | 23.9(-6.3) | 5.32(-5.3) | 23.9(-10.9) | 3.96(+10) | 17.8(+8.5) | 2.7(+8) |
| Panicle removed at 14 DAA (grain devel. stage) | Flag | - | - | | | 25.9(-3.1) | 5.44(-4.8) | 18.8(+1.6) | 3.5(+2.9) |
| | Second | - | - | - | - | 26.6(-2.2) | 5.72(-3.1) | 21.5(+7.5) | 4.3(-2.2) |
| | Third | | | | | 21.3(-1.6) | 3.57(-1.2) | 17.0(+3.7) | 2.6(+4.0) |
| Panicle removed at 21 DAA (grain maturation stage) | Flag | - | - | - | - | | | 17.3(-3.3) | 3.5(-2.9) |
| | Second | - | - | - | - | | | 21.0(+5.0) | 4.4(-0) |
| | Third | | | | | | | 16.0(-2.5) | 2.6(+4) |
| LSD at P = 0.05 | | 0.21 | NS | 0.06 | 0.08 | 0.69 | 0.22 | 0.86 | 0.34 |

Table 24. Effect of panicle removal at different reproductive stages on changes in nitrogen and phosphorus contents (mg.g$^{-1}$. D.W.) in the flag, second and third leaf of rice plant (cv. Kalojira) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (−) over control.

| Treatment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | Nitrogen | Phosphorus | Nitrogen | Phosphorus | Nitrogen | Phosphorus | Nitrogen | Phosphorus |
| Control | Flag | 31.0 | 6.8 | 28.5 | 5.8 | 26.0 | 5.2 | 21.0 | 4.1 |
| | Second | 30.0 | 6.5 | 28.0 | 5.6 | 25.4 | 4.7 | 19.4 | 3.5 |
| | Third | 25.5 | 5.6 | 22.1 | 4.8 | 19.0 | 3.8 | 16.5 | 2.8 |
| Panicle removed at 0 DAA (anthesis stage) | Flag | 31.8(+2.5) | 7.7(+4.4) | 30.2(+6.0) | 6.3(+8.6) | 28.6(+9.0) | 6.03(+15.3) | 23.0(+9.5) | 5.2(+26.8) |
| | Second | 30.3(+1.0) | 6.8(+4.6) | 31.1(+11) | 6.2(+10.7) | 28.0(+13) | 5.4(+14.8) | 22.2(+14.4) | 4.6(+31) |
| | Third | 25.7(+0.8) | 5.8(+4.0) | 24.6(+11.3) | 5.0(+8.3) | 20.7(+8.9) | 4.7(+23) | 18.6(+15) | 3.4(+21) |
| Panicle removed at 7 DAA (grain filling stage) | Flag | − | | 29.6(+3.8) | 5.9(+1.7) | 28.8(+10.7) | 5.8(+11.5) | 23.3(+10.9) | 5.0(+21.9) |
| | Second | − | − | 28.5(+1.7) | 5.7(+1.8) | 27.0(+9.4) | 5.5(+17) | 22.5(+16) | 4.3(+22.8) |
| | Third | | | 23.0(+4.0) | 5.0(+0) | 20.0(+5.4) | 4.4(+17) | 17.8(+7.8) | 3.4(+21) |
| Panicle removed at 14 DAA (grain devet. stage) | Flag | − | − | − | − | 26.8(+3.0) | 5.3(+2.2) | 21.8(+3.8) | 4.3(+9) |
| | Second | | | | | 25.3(+0.8) | 4.5(+1.8) | 19.4(+0) | 3.3(−5.7) |
| | Third | | | | | 18.6(−2.1) | 3.9(+3.1) | 16.6(+0.8) | 2.6(−7.1) |
| Panicle removed at 21 DAA (grain maturation stage) | Flag | − | − | − | − | − | − | 21.6(+3.0) | 4.3(+4.8) |
| | Second | | | | | | | 19.5(+1.5) | 3.6(+2.8) |
| | Third | | | | | | | 16.7(+0.8) | 2.9(+3.5) |
| LSD at P = 0.05 | | 0.06 | 0.11 | 0.36 | 0.09 | 0.56 | 0.09 | 0.34 | 0.47 |

Table 25. Effect of panicle removal at different reproductive stages on changes in nitrogen and phosphorus contents (mg.g$^{-1}$.D.W.) in the flag, second and third leaf of wheat plant (cv. Sonalika) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control.

| Treatment | Leaf position | Days after anthesis | | | | | | | |
| | | 7 | | 14 | | 21 | | 28 | |
| | | Nitrogen | Phosphorus | Nitrogen | Phosphorus | Nitrogen | Phosphorus | Nitrogen | Phosphorus |
| Control | Flag | 26.5 | 6.0 | 24.4 | 5.1 | 22.2 | 3.9 | 16.8 | 3.0 |
| | Second | 25.1 | 5.6 | 23.5 | 4.8 | 19.5 | 3.4 | 15.2 | 2.6 |
| | Third | 23.0 | 4.8 | 18.5 | 4.1 | 16.0 | 3.0 | 14.0 | 2.0 |
| Panicle removed at 0 DAA (anthesis stage) | Flag | 26.9(+1.6) | 6.2(+3.3) | 25.3(+3.6) | 5.8(+13.7) | 24.1(+9) | 4.5(+15.3) | 18.9(+12.5) | 3.66(+22.3) |
| | Second | 25.4(+1.1] | 5.2(+7.1) | 24.2(+2.9) | 5.4(+12.5) | 20.5(+5.2) | 4.1(+20.5) | 16.8(+11) | 3.10(+19.7) |
| | Third | 23.6(+2.6) | 4.6(-4.1) | 18.8(+1.6) | 4.3(+4.6) | 16.6(+3.6) | 3.6(+20) | 14.8(+5.7) | 2.5(+20) |
| Panicle removed at 7 DAA (grain filling stage) | Flag | | | 25.1(+1.6) | 5.11(+1.0) | 22.3(+2.7) | 4.1(+5.0) | 17.8(+6.3) | 3.3(+10) |
| | Second | - | | 24.0(+2.1) | 4.9(+2.0) | 20.3(+4.2) | 3.6(+5.3) | 15.5(+1.9) | 2.9(+13.6) |
| | Third | | - | 18.9(+2.1) | 4.2(+2.4) | 16.8(+5.0) | 3.4(+10) | 14.8(+5.0) | 2.3(+15) |
| Panicle removed at 14 DAA (grain devet. stage) | Flag | | | | | 22.2(+0.4) | 3.8(-3.3) | 17.2(+2.3) | 3.1(+3.1) |
| | Second | - | - | - | - | 19.3(-1.0) | 3.6(+5.8) | 15.4(+1.3) | 2.6(+0) |
| | Third | | | | | 16.2(-2.5) | 3.0(+0) | 13.8(-1.4) | 2.0(+0) |
| Panicle removed at 21 DAA (grain maturation stage) | Flag | | | | | | | 16.6(-1.1) | 2.9(-3.0) |
| | Second | - | - | - | - | - | - | 15.4(+1.3) | 2.6(+7.6) |
| | Third | | | | | | | 14.0(+0) | 2.0(+3) |
| LSD at P = 0.05 | | NS | 0.045 | 0.015 | 0.01 | 0.16 | 0.21 | 0.49 | 0.23 |

Table 26. Effect of panicle removal at different reproductive stages on $[^{32}P]$-phosphate retention by fed leaves (KBq. Leaf$^{-1}$.h$^{-1}$) and stem (when fed through the flag leaf, KBq.g$^{-1}$.F.W.h$^{-1}$) of rice plant (cv. Rasi) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (−) over control.

| Treatment | Leaf position | Days after anthesis | | | |
|---|---|---|---|---|---|
| | | 7 | 14 | 21 | 28 |
| Control | Flag | 350 | 262 | 229 | 158 |
| | Second | 340 | 241 | 245 | 190 |
| | Third | 270 | 208 | 179 | 108 |
| | Stem | 72 | 75 | 73 | 62 |
| Panicle removed at 0 DAA (anthesis stage) | Flag | 320(−8.5) | 295(+12.5) | 254(+11.0) | 220(+39) |
| | Second | 310(−8.8) | 283(+17.0) | 262(+7.0) | 210(+10) |
| | Third | 275(+1.8) | 229(10) | 204(+18) | 33(+25) |
| | Stem | 75(+4.0) | 82(+9) | 80(+10) | 75(+21) |
| Panicle removed at 7 DAA (grain filling stage) | Flag | − | 258(+1.5) | 250(+9.0) | 210(+33) |
| | Second | | 245(+1.6) | 258(+5.8) | 204(+7) |
| | Third | | 220(+1.6) | 208(+16) | 125(+15) |
| | Stem | | 80(+6.6) | 78(+7) | 70(+12) |
| Panicle removed at 14 DAA (grain development stage) | Flag | − | − | 233(+1.7) | 162(+2.5) |
| | Second | | | 241(−1.6) | 195(+2.6) |
| | Third | | | 287(+4.4) | 116(+7.4) |
| | Stem | | | 71(−2.7) | 64(+3.0) |
| Panicle removed at 21 DAA (grain maturation stage) | Flag | − | − | − | 155(−1.8) |
| | Second | | | | 204(+7.3) |
| | Third | | | | 118(+9.2) |
| | Stem | | | | 63(+1.6) |
| LSD at P = 0.05 | | 4.36 | 2.37 | 3.20 | 5.84 |

Table 27. Effect of panicle removal at different reproductive stages on $[^{32}P]$-phosphate retention by the fed leaves (KBq. Leaf$^{-1}$.h$^{-1}$) and stem (when fed through the flag leaf, KBq.g$^{-1}$.F.W.h$^{-1}$) of rice plant (cv. Kalojira) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (−) over control.

| Treatment | Leaf position | Days after anthesis | | | |
|---|---|---|---|---|---|
| | | 7 | 14 | 21 | 28 |
| Control | Flag | 352 | 316 | 270 | 200 |
| | Second | 395 | 308 | 225 | 183 |
| | Third | 308 | 266 | 189 | 133 |
| | Stem | 68 | 70 | 72 | 65 |
| Panicle removed at 0 DAA (anthesis stage) | Flag | 333(−5.3) | 329(+4.1) | 283(+4.8) | 233(+16) |
| | Second | 354(−10) | 325(+5.5) | 241(+7.4) | 216(+18) |
| | Third | 316(−2.5) | 283(+6.2) | 208(+10) | 158(+18) |
| | Stem | 70(+3.0) | 73(+4.2) | 78(+8) | 74(+13) |
| Panicle removed at 7 DAA (grain filling stage) | Flag | − | 310(−1.8) | 287(+6.2) | 229(+14) |
| | Second | − | 295(−4.0) | 250(+10) | 208(+13) |
| | Third | − | 270(+1.5) | 200(+5.8) | 154(+15) |
| | Stem | − | 69(+1.4) | 76(+5.5) | 71(+9) |
| Panicle removed at 14 DAA (grain development stage) | Flag | − | − | 258(+4.4) | 204(+2.0) |
| | Second | − | − | 225(+0) | 179(+2.4) |
| | Third | − | − | 183(−3.1) | 129(+3) |
| | Stem | − | − | 73(+1.3) | 66(+3) |
| Panicle removed at 21 DAA (grain maturation stage) | Flag | − | − | − | 195(+2.5) |
| | Second | − | − | − | 191(+4.3) |
| | Third | − | − | − | 137(+3.0) |
| | Stem | − | − | − | 62(−4.6) |
| LSD at P = 0.05 | | 3.22 | 4.1 | 3.2 | 5.8 |

Table 28. Effect of panicle removal at different reproductive stages on $[^{32}P]$-phosphate retention by the fed leaves (KBq. Leaf$^{-1}$.h$^{-1}$) and stem (when fed through the flag leaf, KBq.g$^{-1}$.F.W.h$^{-1}$) of wheat plant (cv. Sonalika) during the progress of reproductive development. Figures within parentheses indicate percentage increase (+) or decrease (-) over control.

| Treatment | Leaf position | Days after anthesis | | | |
|---|---|---|---|---|---|
| | | 7 | 14 | 21 | 28 |
| Control | Flag | 258 | 245 | 208 | 125 |
| | Second | 266 | 233 | 191 | 108 |
| | Third | 254 | 204 | 137 | 87 |
| | Stem | 64 | 65 | 63 | 60 |
| Panicle removed at 0 DAA (anthesis stage) | Flag | 251(-2.7) | 258(+5.0) | 220(+5.7) | 138(+10) |
| | Second | 258(-3.6) | 241(+3.4) | 204(+6.8) | 125(+15) |
| | Third | 250(-1.5) | 210(+3.0) | 150(+9.4) | 95(+9) |
| | Stem | 66(+3.0) | 69(+6·0) | 66(+4.7) | 70(+14) |
| Panicle removed at 7 DAA (grain filling stage) | Flag | - | 233(-4.9) | 225(+8.0) | 136(+9.8) |
| | Second | - | 225(-3.4) | 200(+4.7) | 116(+7.4) |
| | Third | - | 205(+0.4) | 154(+12) | 95(+9) |
| | Stem | - | 67(+3) | 67(+6.3) | 68(+13) |
| Panicle removed at 14 DAA (grain development stage) | Flag | - | - | 212(-19) | 127(+1.6) |
| | Second | - | - | 187(-2.0) | 105(+2.7) |
| | Third | - | - | 133(+3.0) | 83(-4.5) |
| | Stem | - | - | 64(+1.5) | 62(+3.3) |
| Panicle removed at 21 DAA (grain maturation stage) | Flag | - | - | - | 125(-0) |
| | Second | - | - | - | 104(-3.7) |
| | Third | - | - | - | 85(-2.2) |
| | Stem | - | - | - | 63(+5) |
| LSD at P = 0.05 | | 2.1 | 2.53 | 3.32 | 4.8 |

Table 29. Effect of leaf removal on chlorophyll (Chl) and protein (Prot) contents of the remaining leaves of rice plant (cv. Rasi) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs. 1 & 2.

| Treatment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| Removal of : | | | | | | | | | |
| Flag leaf | Second | +4.2 | +5.5 | -8.5 | -8.4 | -13.7 | -10.2 | -38.0 | -14.5 |
| | Third | +3.7 | +2.8 | -1.8 | -2.4 | - 2.7 | - 2.8 | -10.0 | - 3.1 |
| Second leaf | Flag | +6.84 | +3.4 | -5.0 | -6.4 | -12.3 | -8.2 | -24.0 | -10.6 |
| | Third | +1.2 | +0.8 | -3.2 | -2.1 | -11.0 | -1.6 | - 8.8 | - 4.2 |
| Third leaf | Flag | +0.8 | +1.4 | -1.6 | -1.2 | - 2.4 | -2.6 | -4.8 | -1.4 |
| | Second | +2.5 | +1.2 | -1.2 | -1.6 | - 4.2 | -1.8 | -3.4 | -2.4 |
| LSD at P = 0.05 | | 0.32 | 0.22 | 0.34 | 0.64 | 0.42 | 0.23 | 1.84 | 1.06 |

Table 30. Effect of leaf removal on chlorophyll (Chl) and protein (Prot) content of the remaining leaves of rice plant (cv. Kalojira) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs. 1 & 2.

| Treatment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| Removal of : | | | | | | | | | |
| Flag leaf | Second | +5.1 | +5.3 | -4.1 | -12.0 | -12.5 | -13.2 | -36.0 | -16.0 |
| | Third | +4.6 | +2.1 | -3.1 | - 2.6 | - 4.2 | - 3.1 | -12.0 | - 3.4 |
| Second leaf | Flag | +4.6 | +7.2 | -5.8 | -5.2 | -18.0 | - 7.5 | -22.5 | - 8.9 |
| | Third | +2.3 | +1.6 | -2.6 | -2.4 | - 6.1 | - 2.6 | - 6.3 | - 4.6 |
| Third leaf | Flag | +2.6 | +1.2 | -2.1 | -1.9 | - 8.6 | - 2.1 | - 3.1 | - 4.5 |
| | Second | +2.3 | +1.4 | -1.6 | -3.1 | - 3.8 | - 3.4 | - 4.2 | - 1.8 |
| LSD at P = 0.05 | | 0.21 | 0.14 | 0.08 | 0.67 | 1.87 | 1.03 | 1.63 | 1.77 |

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Table 31. Effect of leaf removal on chlorophyll (Chl) and protein (Prot) contents of the remaining leaves of wheat plant (cv. Sonalika) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Fig.3.

| Treatment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| Removal of : | | | | | | | | | |
| Flag leaf | Second | +3.1 | +3.8 | -5.5 | -7.4 | -7.5 | -8.5 | -18.0 | -8.2 |
| | Third | +1.3 | +1.4 | -2.1 | -2.4 | -1.6 | -2.8 | -4.3 | -2.8 |
| Second leaf | Flag | +4.8 | +1.8 | -3.4 | -3.8 | -8.8 | -4.2 | -10.3 | -3.4 |
| | Third | +3.2 | +1.2 | +1.2 | -2.1 | -2.3 | -1.4 | -2.8 | -1.6 |
| Third leaf | Flag | +2.6 | +0.96 | +1.6 | -0.8 | -1.6 | -3.4 | -3.1 | +2.8 |
| | Second | +1.8 | +1.21 | -2.4 | -1.5 | -2.6 | -1.8 | -3.5 | -1.6 |
| LSD at P = 0.05 | | 0.16 | 0.32 | 0.11 | 0.08 | 0.28 | 0.64 | 1.44 | 1.06 |

Table 32. Effect of leaf removal on nitrogen (N) and phosphorus (P) contents of the remaining leaves of rice plant (cv. Rasi) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (−) over control. For absolute values of the control, see Figs. 8 & 9.

| Treatment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | N | P | N | P | N | P | N | P |
| Removal of : | | | | | | | | | |
| Flag leaf | Second | +3.6 | −9.4 | −5.4 | −9.3 | −8.0 | −14.2 | −15.4 | −26.2 |
| | Third | +0.36 | −1.5 | −1.3 | −2.0 | −0.95 | − 5.2 | − 2.4 | − 8.4 |
| Second leaf | Flag | +2.4 | −5.4 | −3.1 | −4.2 | −6.2 | −7.6 | −8.2 | −14.2 |
| | Third | +0.48 | −1.8 | −0.6 | −0.9 | −2.6 | −2.2 | −1.2 | − 3.6 |
| Third leaf | Flag | +0.32 | −1.3 | −0.8 | −2.2 | −1.2 | −3.7 | −1.0 | − 4.6 |
| | Second | −0.21 | −0.9 | −1.2 | −1.1 | −1.6 | −1.2 | −1.3 | − 2.1 |
| LSD at P = 0.05 | | 0.06 | 0.03 | 0.13 | 0.41 | 0.062 | 1.21 | 1.06 | 1.84 |

Table 33. Effect of leaf removal on nitrogen (N) and phosphorus (P) contents of the remaining leaves of rice plant (cv. Kalojira) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (-) over control. For absolute values of the control, see Figs. 8 & 9 .

| Treatment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | N | P | N | P | N | P | N | P |
| Removal of : | | | | | | | | | |
| Flag leaf | Second | +3.5 | -10.6 | -6.6 | -8.7 | -8.0 | -16.0 | -9.3 | -21.0 |
| | Third | +0.9 | - 3.4 | -2.1 | -4.4 | -2.8 | - 5.2 | -2.1 | - 7.4 |
| Second leaf | Flag | +1.6 | -6.0 | -2.2 | -4.2 | -4.6 | -18.0 | -5.4 | -18.5 |
| | Third | +1.9 | -2.7 | -1.6 | -3.2 | -3.0 | -12.4 | -1.4 | - 6.8 |
| Third leaf | Flag | +2.6 | +2.0 | -1.6 | -1.2 | -2.9 | -2.0 | -1.3 | - 3.1 |
| | Second | +1.4 | -2.8 | -1.42 | -2.8 | -1.2 | -2.4 | -1.8 | - 4.6 |
| LSD at P = 0.05 | | 0.04 | 0.32 | 0.21 | 0.36 | 0.22 | 1.08 | 0.67 | 1.63 |

Table 34. Effect of leaf removal on nitrogen (N) and phosphorus (P) contents of the remaining leaves of wheat plant (cv. Sonalika) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (–) over control. For absolute values of the control, see Figs.8 & 9.

| Treatment | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | N | P | N | P | N | P | N | P |
| Removed of : | | | | | | | | | |
| Flag leaf | Second | +3.4 | -3.7 | -3.3 | -12.8 | -8.2 | -14.0 | -10.6 | -16.5 |
| | Third | +0.86 | -4.2 | -1.6 | -5.0 | -2.64 | -2.8 | -3.4 | -6.0 |
| Second leaf | Flag | +2.6 | -3.4 | -1.8 | -4.0 | -1.2 | -4.2 | -8.5 | -8.7 |
| | Third | +0.8 | -4.3 | -1.1 | -5.8 | -2.4 | -2.1 | -2.3 | -3.9 |
| Third leaf | Flag | -1.8 | -1.7 | -1.85 | -2.0 | -0.9 | -2.2 | -2.2 | -3.8 |
| | Second | -0.4 | -0.6 | -0.86 | -2.1 | -0.85 | -1.8 | -2.6 | -2.4 |
| LSD at P = 0.05 | | 0.04 | 0.12 | 0.06 | 0.21 | 0.16 | 0.20 | 0.35 | 0.87 |

Table 35. Effect of leaf removal on $[^{32}P]$-phosphate mobilization
from the remaining leaves to the grains of rice plant
(cv. Rasi) during the progress of reproductive deve-
lopment. Values are expressed as percentage increase (+)
or decrease (-) over control. For absolute values of
the control, see Fig.10.

| Treatment | Leaf position | Days after anthesis | | | |
|---|---|---|---|---|---|
| | | 7 | 14 | 21 | 28 |
| Removal of : | | | | | |
| Flag leaf | Second | +19.2 | +35.0 | +10.0 | +8.4 |
| | Third | + 9.3 | + 9.0 | + 8.4 | +2.9 |
| Second leaf | Flag | +16.3 | +13.0 | +8.0 | +4.2 |
| | Third | + 4.3 | + 6.0 | +4.1 | +1.4 |
| Third leaf | Flag | + 2.2 | +2.6 | +2.2 | +5.5 |
| | Second | + 3.2 | +4.2 | +3.4 | +2.7 |
| LSD at P = 0.05 | | 1.72 | 2.30 | 1.51 | 0.73 |

Table 36. Effect of leaf removal on [$^{32}$P]-phosphate mobilization
from the remaining leaves to the grains of rice plant
(cv. Kalojira) during the progress of reproductive
development. Values are expressed as percentage
increase (+) or decrease (-) over control. For abso-
lute values of the control, see Fig.10.

| Treatment | Leaf position | Days after anthesis | | | |
|---|---|---|---|---|---|
| | | 7 | 14 | 21 | 28 |
| Removal of : | | | | | |
| Flag leaf | Second | +18.4 | +30.6 | +11.5 | +4.2 |
| | Third | + 6.7 | +11.2 | + 7.8 | +2.6 |
| Second leaf | Flag | +10.8 | +14.2 | +4.3 | +4.3 |
| | Third | + 3.3 | + 2.4 | +3.9 | +3.2 |
| Third leaf | Flag | + 5.8 | + 4.8 | +1.7 | +4.3 |
| | Second | + 3.2 | + 3.2 | +3.2 | +3.7 |
| LSD at P = 0.05 | | 1.84 | 2.64 | 0.62 | 0.33 |

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Table 37. Effect of leaf removal on $[^{32}P]$-phosphate mobilization from the remaining leaves to the grains of wheat plant (cv. Sonalika) during the progress of reproductive development. Values are expressed as percentage increase (+) or decrease (−) over control. For absolute values of the control, see Fig.10.

| Treatment | Leaf position | Days after anthesis | | | |
|---|---|---|---|---|---|
| | | 7 | 14 | 21 | 28 |
| Removal of : | | | | | |
| Flag leaf | Second | +15.3 | +19.7 | +12.0 | +6.8 |
| | Third | + 7.9 | + 7.2 | + 7.0 | +4.7 |
| Second leaf | Flag | + 8.2 | + 8.4 | + 6.8 | +4.9 |
| | Third | + 4.0 | + 4.0 | + 2.4 | +2.6 |
| Third leaf | Flag | + 1.1 | + 1.2 | + 1.8 | +2.4 |
| | Second | + 2.1 | + 1.6 | + 3.4 | +3.7 |
| LSD at P = 0.05 | | 1.59 | 0.82 | 1.53 | 0.44 |

Table 38. Effect of spikelet removal on branch production, leaf area and longevity of the whole plant of rice (cv. Rasi). P = Presence of branch production, A = absence of branch production

| Treatment | Main tiller (MT) | | | | Secondary branch (SB) | | | | Tertiary branch (TB) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Branch produc-tion | Leaf area (cm$^2$) Flag | Leaf area (cm$^2$) Second | Longe-vity of MT (d) | Branch produc-tion | Leaf area (cm$^2$) Flag | Leaf area (cm$^2$) Second | Longe-vity of MT + SB (d) | Branch produc-tion | Leaf area (cm$^2$) Flag | Leaf area (cm$^2$) Second | Total longevity of (MT+SB+ TB) (d) |
| Control (Intact) | A | 28 | 39 | 126 | A | 18 | 19 | 147 | A | 13 | 14 | 166 |
| Removal of : | | | | | | | | | | | | |
| 25% Spikelets | A | 28 | 39 | 126 | A | 18 | 19 | 147 | A | 13 | 14 | 166 |
| 50% Spikelets | P | 28 | 39 | 126 | A | 18 | 19 | 147 | A | 13 | 14 | 166 |
| 75% Spikelets | P | 28 | 39 | 129 | P | 18 | 19 | 149 | A | 13 | 14 | 166 |
| 100% Spikelets | P | 28 | 39 | 133 | P | 18 | 19 | 154 | A | 13 | 14 | 173 |
| Emasculated | P | 28 | 39 | 133 | P | 18 | 19 | 154 | A | 13 | 14 | 173 |
| Second leaf + 100% Spikelets | A | - | - | - | A | - | - | - | A | - | - | - |

Table 39. Effect of spikelet removal on branch production, leaf area and longevity of the whole plant of rice (cv. Kalojira). A = Absence of branch production, P = Presence of branch production.

| Treatment | Main tiller (MT) | | | | Secondary branch (SB) | | | | Tertiary branch (TB) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Branch produc-tion | Leaf area(cm²) Flag | Leaf area(cm²) Second | Longe-vity of MT (d) | Branch produc-tion | Leaf area(cm²) Flag | Leaf area(cm²) Second | Longe-vity of (MT+SB) (d) | Branch produc-tion | Leaf area(cm²) Flag | Leaf area(cm²) Second | Total lon-gevity of (MT+SB+TB) (d) |
| Control (Intact) | A | 36 | 45 | 142 | A | 24 | 28 | 159 | A | 15 | 16 | 179 |
| Removal of : | | | | | | | | | | | | |
| 25% Spikelets | A | 36 | 45 | 142 | A | 24 | 28 | 159 | A | 15 | 16 | 179 |
| 50% Spikelets | P | 36 | 45 | 142 | A | 24 | 28 | 159 | A | 15 | 16 | 179 |
| 75% Spikelets | P | 36 | 45 | 146 | P | 24 | 28 | 163 | A | 15 | 16 | 182 |
| 100% Spikelets | P | 36 | 45 | 149 | P | 24 | 28 | 166 | A | 15 | 16 | 186 |
| Emasculated | P | 36 | 45 | 149 | P | 24 | 28 | 166 | A | 15 | 16 | 186 |
| Second leaf + 100% Spikelets | A | - | - | - | A | - | - | - | A | - | - | - |

Table 40. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents ($mg.g^{-1}$ . F.W.) in the flag, second and third leaf of main tiller of rice plant (cv. Rasi) during the progress of reproductive development.

| Percentage removal of spikelets | Leaf Position | Days after anthesis | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | 7 | | 14 | | 21 | | 28 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| 0 (Control) | Flag | 1.18 | 78.4 | 0.73 | 64.8 | 0.31 | 51.8 | 0.08 | 39.8 |
| | Second | 0.95 | 65.9 | 0.62 | 60.3 | 0.34 | 49.4 | 0.13 | 43.9 |
| | Third | 0.74 | 60.3 | 0.54 | 54.5 | 0.17 | 42.2 | 0.04 | 34.3 |
| 25 | Flag | 1.10 | 81.6 | 0.75 | 64.3 | 0.32 | 50.6 | 0.082 | 40.2 |
| | Second | 0.94 | 66.7 | 0.65 | 61.8 | 0.33 | 47.8 | 0.12 | 44.2 |
| | Third | 0.71 | 58.9 | 0.51 | 52.3 | 0.18 | 40.8 | 0.045 | 35.2 |
| 50 | Flag | 1.08 | 76.1 | 0.76 | 65.1 | 0.36 | 54.8 | 0.14 | 46.6 |
| | Second | 0.96 | 71.5 | 0.61 | 62.3 | 0.34 | 48.3 | 0.13 | 45.7 |
| | Third | 0.69 | 59.5 | 0.53 | 55.1 | 0.16 | 43.1 | 0.06 | 33.9 |
| 75 | Flag | 1.01 | 76.9 | 0.83 | 66.6 | 0.39 | 55.1 | 0.15 | 50.5 |
| | Second | 0.96 | 68.7 | 0.64 | 62.5 | 0.36 | 53.3 | 0.14 | 48.1 |
| | Third | 0.73 | 61.2 | 0.55 | 54.2 | 0.18 | 42.5 | 0.05 | 36.5 |
| 100 | Flag | 1.11 | 80.1 | 0.80 | 68.1 | 0.47 | 60.2 | 0.21 | 52.7 |
| | Second | 0.92 | 72.3 | 0.62 | 58.4 | 0.37 | 55.5 | 0.18 | 49.3 |
| | Third | 0.70 | 60.5 | 0.56 | 53.3 | 0.18 | 44.1 | 0.07 | 36.1 |
| Emasculated | Flag | 1.03 | 80.2 | 0.81 | 67.0 | 0.41 | 62.8 | 0.21 | 51.3 |
| | Second | 0.98 | 74.9 | 0.65 | 60.6 | 0.36 | 56.1 | 0.17 | 50.7 |
| | Third | 0.68 | 57.9 | 0.55 | 56.1 | 0.175 | 43.8 | 0.065 | 37.7 |
| LSD at P = 0.05 | | 0.0043 | 0.27 | 0.0064 | 0.47 | 0.008 | 1.03 | 0.009 | 1.07 |

Table 41. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g$^{-1}$. F.W.) in the flag, second and third leaf of main tiller of rice plant (cv. Kalojira) during the progress of reproductive development.

| Percentage removal of spikelets | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| 0 (Control) | Flag | 1.10 | 83.5 | 0.82 | 69.0 | 0.54 | 58.0 | 0.29 | 48.0 |
| | Second | 0.94 | 76.2 | 0.71 | 62.0 | 0.49 | 54.0 | 0.21 | 45.0 |
| | Third | 0.75 | 62.2 | 0.51 | 56.0 | 0.24 | 48.0 | 0.08 | 39.0 |
| 25 | Flag | 1.03 | 82.2 | 0.80 | 70.1 | 0.53 | 57.0 | 0.28 | 48.9 |
| | Second | 0.91 | 75.5 | 0.70 | 62.3 | 0.51 | 55.0 | 0.22 | 44.2 |
| | Third | 0.73 | 64.3 | 0.52 | 55.5 | 0.23 | 47.0 | 0.08 | 38.8 |
| 50 | Flag | 1.02 | 78.5 | 0.83 | 70.3 | 0.56 | 60.0 | 0.32 | 51.3 |
| | Second | 0.93 | 77.2 | 0.72 | 64.0 | 0.54 | 55.0 | 0.24 | 47.5 |
| | Third | 0.71 | 60.3 | 0.50 | 57.1 | 0.23 | 49.5 | 0.09 | 39.9 |
| 75 | Flag | 1.06 | 77.1 | 0.86 | 72.3 | 0.58 | 63.4 | 0.36 | 53.4 |
| | Second | 0.92 | 74.1 | 0.74 | 66.8 | 0.54 | 56.6 | 0.26 | 47.4 |
| | Third | 0.74 | 61.1 | 0.53 | 58.5 | 0.76 | 50.1 | 0.095 | 41.2 |
| 100 | Flag | 1.07 | 79.2 | 0.85 | 75.1 | 0.61 | 64.5 | 0.41 | 57.1 |
| | Second | 0.95 | 73.4 | 0.75 | 65.2 | 0.58 | 57.3 | 0.31 | 49.2 |
| | Third | 0.75 | 60.4 | 0.54 | 58.0 | 0.28 | 52.2 | 0.10 | 44.5 |
| Emasculated | Flag | 1.05 | 76.5 | 0.84 | 74.5 | 0.62 | 63.5 | 0.38 | 56.5 |
| | Second | 0.92 | 71.5 | 0.75 | 64.6 | 0.57 | 58.4 | 0.33 | 50.5 |
| | Third | 0.72 | 61.8 | 0.53 | 57.5 | 0.27 | 54.1 | 0.11 | 45.3 |
| LSD at P = 0.05 | | NS | 0.46 | 0.006 | 0.42 | 0.0084 | 0.64 | 0.0072 | 0.74 |

Table 42. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g$^{-1}$, F.W.) in the flag, second and third leaf of main tiller of wheat plant (cv. Sonalika) during the progress of reproductive development.

| Percentage removal of spikelets | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| 0 (Control) | Flag | 1.09 | 64.0 | 0.74 | 58.0 | 0.46 | 49.2 | 0.23 | 39.0 |
| | Second | 1.01 | 60.0 | 0.72 | 52.0 | 0.37 | 44.0 | 0.16 | 35.0 |
| | Third | 0.79 | 54.5 | 0.53 | 47.0 | 0.21 | 39.5 | 0.04 | 30.5 |
| 25 | Flag | 1.06 | 62.2 | 0.75 | 57.0 | 0.47 | 50.5 | 0.21 | 40.0 |
| | Second | 1.00 | 60.4 | 0.71 | 51.0 | 0.36 | 44.0 | 0.17 | 35.4 |
| | Third | 0.80 | 55.5 | 0.51 | 48.0 | 0.22 | 38.3 | 0.03 | 31.0 |
| 50 | Flag | 1.03 | 65.0 | 0.77 | 59.0 | 0.45 | 48.0 | 0.24 | 40.2 |
| | Second | 0.98 | 60.3 | 0.71 | 54.0 | 0.35 | 45.4 | 0.17 | 36.2 |
| | Third | 0.76 | 54.5 | 0.52 | 47.0 | 0.22 | 40.2 | 0.05 | 32.1 |
| 75 | Flag | 1.05 | 61.6 | 0.74 | 59.5 | 0.48 | 51.0 | 0.24 | 41.5 |
| | Second | 1.01 | 59.0 | 0.72 | 53.2 | 0.38 | 43.0 | 0.18 | 37.2 |
| | Third | 0.78 | 55.7 | 0.54 | 48.1 | 0.21 | 40.4 | 0.06 | 31.8 |
| 100 | Flag | 1.03 | 62.5 | 0.79 | 60.3 | 0.52 | 54.0 | 0.31 | 44.8 |
| | Second | 0.99 | 58.0 | 0.75 | 58.2 | 0.40 | 47.5 | 0.24 | 40.5 |
| | Third | 0.75 | 56.0 | 0.53 | 50.3 | 0.24 | 40.0 | 0.07 | 33.5 |
| Emasculated | Flag | 1.03 | 63.0 | 0.78 | 61.1 | 0.54 | 53.2 | 0.29 | 45.1 |
| | Second | 0.94 | 58.0 | 0.73 | 57.7 | 0.39 | 48.6 | 0.24 | 42.5 |
| | Third | 0.78 | 55.2 | 0.55 | 49.2 | 0.26 | 41.0 | 0.08 | 34.8 |
| LSD at P = 0.05 | | NS | 0.32 | 0.0051 | 0.44 | 0.003 | 0.45 | 0.006 | 0.52 |

Table 43. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g$^{-1}$. FW) in the flag and second leaf of secondary branch of rice plant (cv. Rasi) during the progress of reproductive development.

| Percentage removal of spikelets | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| 0 (Control) | Flag | 0.99 | 72.2 | 0.71 | 62.9 | 0.29 | 50.2 | 0.11 | 38.2 |
| | Second | 0.91 | 70.2 | 0.66 | 58.5 | 0.28 | 48.3 | 0.16 | 42.6 |
| 25 | Flag | 0.93 | 73.2 | 0.68 | 63.6 | 0.306 | 52.1 | 0.11 | 38.5 |
| | Second | 0.94 | 71.1 | 0.65 | 58.8 | 0.29 | 47.7 | 0.175 | 43.7 |
| 50 | Flag | 0.98 | 75.8 | 0.69 | 60.4 | 0.34 | 52.4 | 0.13 | 42.0 |
| | Second | 0.91 | 69.3 | 0.69 | 59.9 | 0.33 | 50.3 | 0.165 | 44.5 |
| 75 | Flag | 0.92 | 75.3 | 0.72 | 66.3 | 0.37 | 56.0 | 0.16 | 48.3 |
| | Second | 0.92 | 69.3 | 0.66 | 60.1 | 0.34 | 52.2 | 0.162 | 44.65 |
| 100 | Flag | 0.92 | 76.3 | 0.72 | 67.3 | 0.394 | 60.2 | 0.192 | 51.9 |
| | Second | 0.93 | 64.1 | 0.67 | 58.5 | 0.34 | 55.3 | 0.185 | 47.8 |
| Emasculated | Flag | 0.96 | 76.1 | 0.75 | 67.3 | 0.39 | 59.2 | 0.19 | 50.7 |
| | Second | 0.93 | 66.6 | 0.65 | 60.3 | 0.35 | 58.8 | 0.16 | 48.5 |
| LSD at P = 0.05 | | 0.0063 | 0.87 | 0.005 | 0.42 | 0.0074 | 1.06 | 0.80 | 1.36 |

Table 44. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents ($mg.g^{-1}$. FW) in the flag and second leaf of secondary branch of rice plant (cv. Kalojira) during the progress of reproductive development.

| Percentage removal of spikelets | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| 0 (Control) | Flag | 0.98 | 80.3 | 0.80 | 67.0 | 0.52 | 54.0 | 0.18 | 43.0 |
| | Second | 0.91 | 74.5 | 0.72 | 61.0 | 0.46 | 49.0 | 0.14 | 38.2 |
| 25 | Flag | 0.96 | 79.5 | 0.81 | 66.5 | 0.50 | 53.0 | 0.17 | 44.0 |
| | Second | 0.92 | 73.5 | 0.70 | 60.2 | 0.47 | 50.2 | 0.14 | 38.5 |
| 50 | Flag | 0.97 | 78.5 | 0.80 | 66.4 | 0.52 | 58.0 | 0.21 | 44.0 |
| | Second | 0.90 | 72.8 | 0.71 | 62.3 | 0.47 | 53.3 | 0.15 | 40.5 |
| 75 | Flag | 0.95 | 77.9 | 0.82 | 68.7 | 0.54 | 57.0 | 0.26 | 46.0 |
| | Second | 0.89 | 74.4 | 0.70 | 63.2 | 0.48 | 54.4 | 0.21 | 41.5 |
| 100 | Flag | 0.96 | 76.5 | 0.84 | 69.9 | 0.58 | 61.0 | 0.31 | 52.0 |
| | Second | 0.91 | 70.3 | 0.72 | 64.5 | 0.51 | 55.0 | 0.22 | 45.6 |
| Emasculated | Flag | 0.92 | 75.3 | 0.83 | 69.4 | 0.57 | 60.2 | 0.30 | 51.0 |
| | Second | 0.90 | 71.3 | 0.72 | 64.8 | 0.52 | 56.0 | 0.25 | 45.0 |
| LSD at 0 = 0.05 | | NS | 0.46 | 0.003 | 0.64 | 0.006 | 0.78 | 0.008 | 0.84 |

Table 45. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g$^{-1}$. FW) in the flag and second leaf of tertiary branch of rice plant (cv. Rasi) during the progress of reproductive development

| Percentage removal of spikelets | Leaf position | Days after anthesis | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | 7 | | 14 | | 21 | | 28 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| 0 (Control) | Flag | 0.89 | 73.2 | 0.71 | 62.2 | 0.30 | 51.1 | 0.09 | 38.2 |
| | Second | 0.86 | 70.2 | 0.57 | 58.3 | 0.26 | 48.2 | 0.15 | 42.3 |
| 25 | Flag | 0.88 | 74.3 | 0.70 | 62.3 | 0.304 | 52.3 | 0.08 | 38.9 |
| | Second | 0.86 | 70.5 | 0.59 | 57.2 | 0.25 | 48.8 | 0.14 | 41.1 |
| 50 | Flag | 0.91 | 70.2 | 0.65 | 60.3 | 0.31 | 53.7 | 0.11 | 39.0 |
| | Second | 0.85 | 71.9 | 0.64 | 57.7 | 0.27 | 50.3 | 0.16 | 42.2 |
| 75 | Flag | 0.95 | 79.2 | 0.69 | 65.5 | 0.33 | 58.1 | 0.14 | 44.5 |
| | Second | 0.93 | 72.7 | 0.66 | 63.3 | 0.32 | 51.1 | 0.18 | 44.9 |
| 100 | Flag | 0.95 | 81.1 | 0.73 | 67.7 | 0.35 | 58.2 | 0.17 | 46.5 |
| | Second | 0.94 | 73.3 | 0.66 | 64.6 | 0.34 | 52.5 | 0.19 | 48.5 |
| Emasculated | Flag | 0.91 | 75.6 | 0.74 | 66.6 | 0.33 | 57.7 | 0.16 | 45.1 |
| | Second | 0.90 | 75.2 | 0.65 | 65.0 | 0.32 | 54.9 | 0.17 | 47.3 |
| LSD at P = 0.05 | | 0.0084 | 0.64 | 0.009 | 0.94 | 0.004 | 0.71 | 0.01 | 0.66 |

Table 46. Effect of different percentage of spikelet removal or emasculation treatment on changes in chlorophyll (Chl) and protein (Prot) contents (mg.g$^{-1}$. FW) in the flag and second leaf of tertiary branch of rice plant (cv. Kalojira) during the progress of reproductive development.

| Percentage removal of spikelets | Leaf position | Days after anthesis | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 7 | | 14 | | 21 | | 28 | |
| | | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. | Chl. | Prot. |
| 0 (Control) | Flag | 0.96 | 74.0 | 0.79 | 63.0 | 0.50 | 50.0 | 0.18 | 40.0 |
| | Second | 0.90 | 72.0 | 0.68 | 58.0 | 0.47 | 47.0 | 0.14 | 35.0 |
| 25 | Flag | 0.95 | 71.0 | 0.78 | 64.0 | 0.49 | 51.0 | 0.18 | 41.0 |
| | Second | 0.91 | 70.0 | 0.65 | 58.0 | 0.46 | 46.0 | 0.15 | 35.7 |
| 50 | Flag | 0.97 | 70.5 | 0.79 | 62.0 | 0.51 | 51.0 | 0.19 | 40.2 |
| | Second | 0.92 | 70.0 | 0.67 | 59.0 | 0.47 | 47.0 | 0.15 | 36.7 |
| 75 | Flag | 0.95 | 71.2 | 0.78 | 65.0 | 0.54 | 56.0 | 0.21 | 42.0 |
| | Second | 0.89 | 70.3 | 0.69 | 59.0 | 0.51 | 51.0 | 0.19 | 40.0 |
| 100 | Flag | 0.98 | 72.0 | 0.79 | 66.0 | 0.55 | 58.0 | 0.26 | 46.5 |
| | Second | 0.90 | 69.0 | 0.70 | 62.0 | 0.52 | 52.0 | 0.22 | 42.0 |
| Emasculated | Flag | 0.94 | 71.5 | 0.78 | 65.0 | 0.56 | 57.0 | 0.28 | 48.4 |
| | Second | 0.90 | 69.2 | 0.70 | 60.0 | 0.52 | 53.0 | 0.23 | 43.6 |
| LSD at P = 0.05 | | NS | 0.34 | 0.004 | 0.38 | 0.006 | 0.72 | 0.007 | 0.84 |

Table 47.  Effect of different treatments on whole plant senescence of two rice and one wheat cultivars.

| Species | Cultivar | Treatment | Delay of senescence over control in days |
|---------|----------|-----------|------------------------------------------|
| Rice | Rasi | BA | 7 |
| | | $(BA + GA_3)$ | 10 |
| | | Panicle removed at the anthesis stage | 10 |
| | | 100% Spikelet removed from the main tiller | 9 |
| | | Main tiller with secondary branch | 28 |
| | | Main tiller with secondary and tertiary branch | 44 |
| | Kalojira | BA | 7 |
| | | $(BA + GA_3)$ | 11 |
| | | Panicle removed at the anthesis stage | 12 |
| | | 100% Spikelet removed from the main tiller | 12 |
| | | Main tiller with secondary branch | 24 |
| | | Main tiller with secondary and tertiary branch | 42 |
| Wheat | Sonalika | BA | 7 |
| | | $(BA + GA_3)$ | 10 |
| | | Panicle removed at the anthesis stage | 6 |
| | | 100% Spikelet removed | 7 |
| | | (No secondary or tertiary branch developed) | |

Table 48. Effect of normal and .unfavourable photoperiod on flowering and senescence of four photoperiod sensitive rice cultivars.

| Cultivar | Appearance of anthesis at the plant age under | |
| --- | --- | --- |
| | Favourable photoperiod | Unfavourable photoperiod |
| Kalojira | 115 | 304 |
| Badsabhog | 116 | 300 |
| Patnai | 120 | 312 |
| Kalma | 118 | 310 |

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